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The Canadian Entomologist

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Some Characteristics of Simple Types of Predation and Parasitism[1]

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In an earlier study (Holling, 1959) the basic and subsidiary components of predation were demonstrated in a predator-prey situation involving the predation of sawfly cocoons by small mammals. One of the basic components, termed the functional response, was a response of the consumption of prey by individual predators to changes of prey density, and it appeared to be at least theoretically important in population regulation. Because of this importance the functional response has been further examined in an attempt to explain its characteristics.

The analytical approach adopted required a predator-prey situation in which the functional response was basically simple and from which more complex types could be developed. An explanation of the basic response would then be the first step towards an explanation of more complex ones, such as those already demonstrated by the small mammals. Artificial predator-prey situations were devised which were found to meet these requirements, and the mathematical equation derived to explain the basic response also appeared to describe the published data concerning the effect of host density upon the number of hosts attacked by insect parasites.

Artificial Predator-Prey Situations

In the first artificial situation devised the "prey" were sandpaper discs four centimetres in diameter thumb-tacked to a three-foot square table. A blindfolded subject, the 'predator', stood in front of the table and searched for the discs for one minute by tapping with her finger. As each disc was found, it was removed, set to one side and searching continued. Each experiment was replicated eight times at densities of discs ranging from four to 256 per nine sq. ft.

The results of one such experiment are shown in Fig. 1, where it can be seen that the number of discs picked up increased at a progressively decreasing rate as the density of discs rose. At first thought one might expect a linear relationship, so that a doubling of the density of discs would result in a doubling of the number of discs picked up. The explanation for the departure from linearity might well involve the time that must be taken to pick up discs and dispose of them, in that at the higher densities, when large numbers of discs are located, a large proportion of the available time must be spent, not in searching, but in removing discs from the table. As a result, the apparent rate of discovery would be lower than at the lower densities where very few discs were found and most of the time available could be spent in actively searching for them.

Assuming this explanation to be correct, the simplest expression of the relationship is

$$y = aT_s x \qquad (1)$$

where y is the number of discs removed, x is the density of discs, T_s is the time available for searching, and a is a constant equal to the rate of searching multiplied by the probability of finding a given disc. This constant will be termed the instantaneous rate of discovery. If a fixed interval of time, T_t, is allowed for

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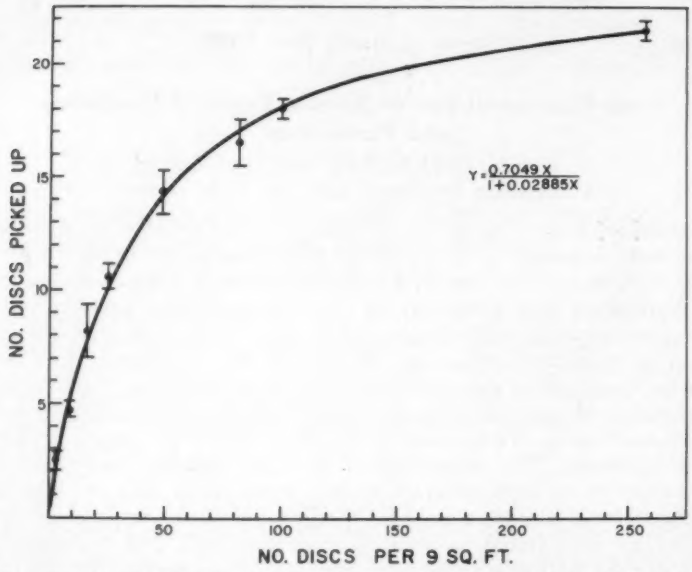

Fig. 1. Functional response of a subject searching for sandpaper discs by touch. (Averages ± 2 S.E. of 8 replicates.)

one experiment, T_s must vary with the number of discs found, for the time taken to remove discs decreases the searching time. Thus, if b equals the time to pick up one disc, then

$$T_s = T_t - by \tag{2}$$

Substituting (2) in (1)

$$y = a(T_t - by)x \tag{3}$$

which simplifies to

$$y = \frac{T_t ax}{1 + abx} \tag{4}$$

When the constants a and b are not directly measured they can be calculated by transforming (4) into a straight-line equation:

$$\frac{y}{x} = -aby + T_t a \tag{5}$$

When $\frac{y}{x}$ is plotted against y the slope of the line fitted by the least squares method is equal to $-ab$, and the intercept on the ordinate is equal to $T_t a$. The data illustrated in Fig. 1 were used to calculate a and b and the curve in the figure is based on equation (4) above. It is obvious that the curve describes the data very well; the departure of the observed from the calculated points is not significant ($P>99\%$).

Even though the equation describes the data well, final proof that it is correct will only come when the assumptions upon which the equation is based are tested and proved. There are two such assumptions, i.e., that a, the instantaneous rate of

TABLE I.

Effect of density upon the instantaneous rate of discovery and the time to pick up each disc in experiment 1. Figures represent the averages ± 1 S. E. of eight replicates.

No. of discs per 9 sq. ft. x	Inst. rate of discovery a	Time to pick up 1 disc b
4	0.705 ± 0.050	0.0439 ± 0.0013
9	0.675 ± 0.075	0.0431 ± 0.0013
16	0.799 ± 0.081	0.0415 ± 0.0052
25	0.757 ± 0.030	0.0411 ± 0.0013
49	0.739 ± 0.040	0.0415 ± 0.0011
81	0.634 ± 0.032	0.0412 ± 0.0012
100	0.720 ± 0.079	0.0405 ± 0.0013
256	0.762 ± 0.105	0.0408 ± 0.0006

discovery, and *b*, the time taken to pick up one disc, are both constant at all prey densities. These two assumed constants were independently measured in an identical experiment and the results are presented in Table I. It requires no recourse to statistics to see that *a* and *b* are indeed constants, unaffected by changes of disc density. These measured values of *a* and *b* are almost identical to the values calculated from equation (5), i.e. 0.71 and 0.041 respectively. Hence it seems that this artificial situation demonstrates an extremely simple type of functional response where only two simply-operating, time-consuming behaviours – searching and handling of prey – are necessary to describe its characteristics. Moreover, it is a *basic* type, for it is difficult to imagine any predator-prey situation where at least these two behaviours are not involved.

With such a simple and easily measured functional response available it was then possible to manipulate the experiment in the hopes that some clues could be obtained to the explanation of more complicated functional responses. This was done by having the subject use a different and more ambiguous sense to locate the discs. In the experiment already described, the sense of touch was used – a very positive sense. In the next series of experiments the sense of hearing was used. These experiments were identical to the ones already described except that the subject, instead of searching for the discs with her finger, located them with the blunt end of a pencil during a two minute interval. Data from these experiments are presented in Fig. 2 and they closely resemble those already presented (Fig. 1). The curve is based on equation (4) and again the departure of the observed points from the calculated is not significant ($P>99\%$). An additional set of data, obtained using a different subject as the "predator", was almost identical.

Although the validity of the equation had already been established when the sense of touch was used to locate discs, it again seemed worth while to measure the values of *a* and *b*. These measurements are presented in Table II and it is apparent that *b* was again constant, although slightly higher than before since handling the pencil made it harder to pick up the discs. Strangely, however, *a* was definitely affected by increase in prey density, decreasing in a regular manner from 0.387 to 0.100. Other anomalies are also apparent for, unlike the first experiment, the values of *a* and *b* calculated from equation (5) (0.37 and 0.075 respectively) are quite different from the values that were actually measured. This is to be expected for *a* because of its variability, but the measured values of *b*, although constant, were lower than the calculated value.

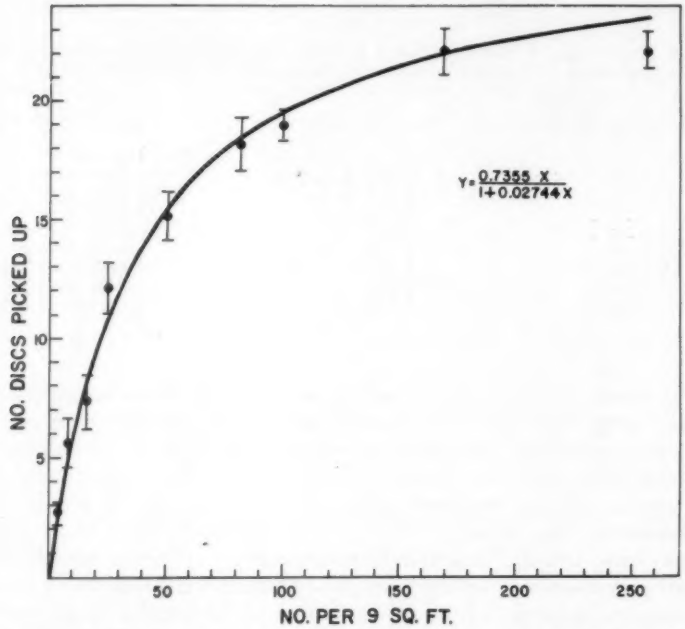

Fig. 2. Functional response of a subject searching for sandpaper discs by sound. (Averages ± 2 S.E. of 8 replicates.)

The variability of *a* presents a paradox, for even though it does vary, equation (4), which was derived from the assumption that *a* was a constant, describes the data with satisfactory accuracy. The precise nature of this equation thus seems to be broader than it first appeared, and it is necessary now to explore its characteristics further. If *b* varied with changes of disc density the equation would not describe the data unless *a* varied in such a way as to mask the variability of *b*. On the other hand it is possible that *a* could vary in a very particular fashion so that the equation would still fit. Imagine a simple situation, for example, where *b* equals zero and *a* decreases with increasing disc density. The resulting curve

TABLE II.

Effect of density upon the instantaneous rate of discovery and the time to pick up each disc in experiment 2. Figures represent the averages ± 1 S. E. of eight replicates.

No. discs per 9 sq. ft. x	Inst. rate of discovery a	Time to pick up 1 disc. b
4	0.387 ± 0.032	0.0496 ± 0.0012
9	0.370 ± 0.040	0.0518 ± 0.0013
16	0.284 ± 0.024	0.0496 ± 0.0012
25	0.345 ± 0.028	0.0476 ± 0.0011
49	0.254 ± 0.039	0.0504 ± 0.0009
81	0.201 ± 0.089	0.0480 ± 0.0010
100	0.176 ± 0.006	0.0482 ± 0.0007
169	0.144 ± 0.024	0.0495 ± 0.0010
256	0.100 ± 0.005	0.0508 ± 0.0011

would have a continually decreasing slope and would resemble the curves obtained when a and b were constants with b greater than zero. Furthermore, particular functions of x that a might take would render the two curves indistinguishable, so that the proposed equation would apply to both.

In order for a to vary in this particular fashion, the basic characteristics of equation (3) must remain unchanged. This can be achieved by separating a into two constants, a' and c, with c affecting the variable y so that equation (3) is basically the same. Thus

$$y = a'(T_t - (b + c)y)x \tag{6}$$

which simplifies to

$$y = \frac{T_t a x}{1 + (b + c)x} \tag{7}$$

In words, this states that an additional time-consuming behaviour is operating that reduces the time available for searching by a fixed amount, c, for each disc picked up. In the present experiment this new behaviour appeared to arise from the difficulty the "predator" experienced in making a positive identification of a disc by the sound made when it was touched by the pencil. Close observation showed that when a disc was touched there was a distinct hesitation during which the subject tapped rapidly with the pencil in order to confirm the fact that a disc had indeed been located. Thus an additional component – identification time – is added to the two basic ones of searching and handling of prey.

From equation (6) it is now possible to derive the precise relationship a must have with x. The constant b in this equation is not involved in a, the instantaneous rate of discovery, and can be expressed in terms of a, y, and x, from (3). That is

$$b = \frac{T_t a x - y}{a y x} \tag{8}$$

Substituting (8) in (6) we get

$$y = T_t a' x - a' yx\left(\frac{T_t ax - y}{a y x}\right) - a' cy$$

which simplifies to

$$a = \frac{a'}{1 + a'cx} \tag{9}$$

This is the specific relationship a must have with x if equation (4) is to describe accurately a set of data. The simplest condition prevails when the identification of prey is virtually instantaneous, as was the case in the experiment where the discs were located by touch, for then $c = 0$ and $a = a'$, a constant. Unless a is actually measured, however, there is no way to determine whether it is a constant. If equation (4) is found to describe accurately an observed set of data, this indicates that a is either a constant or varies in the way expressed by (9).

If a is actually measured, however, equation (9) can be transformed into

$$\frac{1}{a} = cx + \frac{1}{a'} \tag{10}$$

and a plot of $1/a$ against x should yield a straight line whose slope equals c, the identification time factor. The degree to which equation (4) describes a functional response will be reflected by the closeness of fit of the observed points to

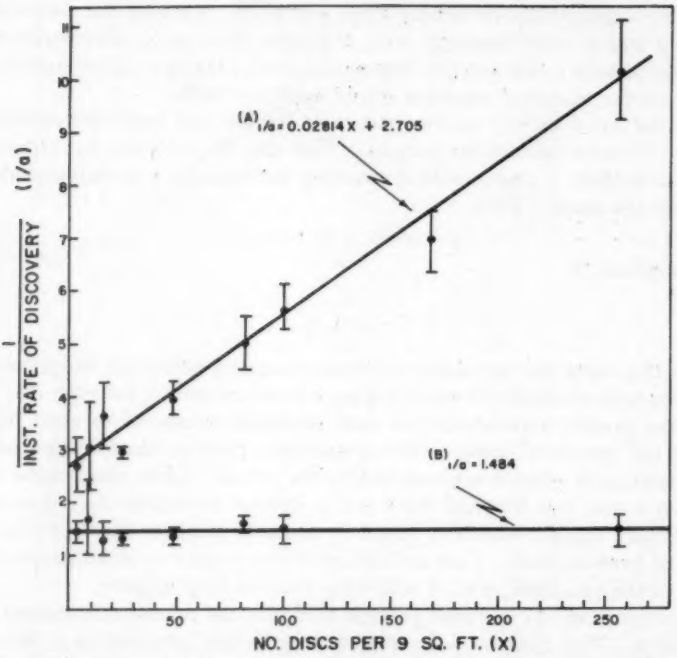

Fig. 3. Effect of disc density upon the instantaneous rate of discovery. (Averages ± 2 S.E. of 8 replicates.)

this straight line. The values of $1/a$ for the two experiments already described are plotted against x in Fig. 3. When the sense of touch was used to locate the discs the line (B) runs parallel to the axis of abscissa so that the slope, or c, equals 0. That is, no measurable time was taken to identify discs. When the sense of hearing was used to locate discs, the points lie along a sloping straight line (A) in the manner predicted by equation (9). The slope of this line, 0.028, is the number of minutes taken in hesitating over each disc. This provides the explanation for the high value of b as calculated from equation (5), since the identification time factor, c (0.028), was incorporated with the actual value of b (0.049). These two measured values of b and c add to give 0.077, very similar to the value 0.075 calculated from equation (5).

Before proceeding to natural predator-prey situations, it is worth while to recapitulate the conclusions arising from the artificial situations. In the first of these only two time-consuming behaviours – searching and handling of prey – determined the form of the functional response, and neither of these behaviours acted concurrently. That is, while the prey were being handled, searching stopped. Moreover, these two activities acted in the simplest possible fashion so that both the rate of searching and the time spent in handling prey was a constant at all "prey" densities. Since all predator-prey situations must involve at least these two behaviours, this functional response represents a *basic* type from which more complex ones can be derived, and equation (4) is hence the *basic functional response equation.*

One of these more complex types was demonstrated in the second artificial situation in which the discs were located by the sense of hearing. In this case a third time-consuming component, identification time, was added to the two basic activities. This component acted in a very simple fashion, by decreasing the time available for searching by a certain fixed amount for each disc discovered. As a result of this experiment, it became clear that the basic equation (4) would hold not only when *a* and *b* were constant, but also when *a* varied in the very precise fashion described in equation (9) and *b* was again a constant.

The effects of three time-consuming behaviours have thus far been described, but other components might also affect the functional response in natural situations. The ones that first come to mind concern satiation in the case of predators, and egg complement in the case of parasites. Both these factors will place an ultimate upper limit on the functional response and will affect the rising phase as well. Their effect might well be expressed in the time taken in resting – an additional time-consuming behaviour. Thus as the predator becomes more satiated and as the parasite runs out of eggs more and more time would be spent in resting. If the amount of this time was directly proportional to the number of prey or hosts attacked, then the basic equation (4) could be simply rewritten as

$$y = \frac{T_t a x}{1 + (b + d) x}$$

where *d* is the time spent resting on each prey or host. This is of course basically the same as equation (4) and (7). Other possibilities also exist, however, and the true explanation must await further experiments which independently measure the effects of separate components.

Natural Predator-Prey Situations

In order to apply the basic functional response equation to natural situations, the density of predators or parasites must be constant, the density of hosts or prey must be measured, and the number of hosts or prey attacked in a given period of time must be known. The only true predator-prey information of this sort available in the published literature is for small mammals preying upon sawfly cocoons (Holling, 1959).

Each of the functional responses demonstrated by small mammals under these conditions shows an S-shaped rise up to a maximum consumption. Hence it is pointless to apply equation (4) since this equation predicts a continually decreasing slope. Apparently an additional component is affecting the response by causing the searching rate to be stimulated by each prey found. Experiments are now being conducted to investigate this possibility. There is, however, a considerable body of parasite-host information available in the literature, and inspection of this shows functional responses at least visually similar to those demonstrated in the disc experiments.

Burnett's series of experiments (Burnett, 1951, 1954, 1958), in which fixed numbers of *Dahlbominus fuliginosus* (Nees) [under the name *fuscipennis* (Zett.)] searched for sawfly cocoons at various densities, are particularly appropriate to test the validity of a mathematical model, for they range from laboratory conditions, through semi-natural conditions when the parasite searched on a lawn, to natural conditions when the parasites searched in a mixed woodlot. The results of his laboratory experiments (Burnett, 1951) are shown in Fig. 4, where each of the four graphs represents the functional response obtained under different experimental conditions. The lines drawn through the points are based upon the

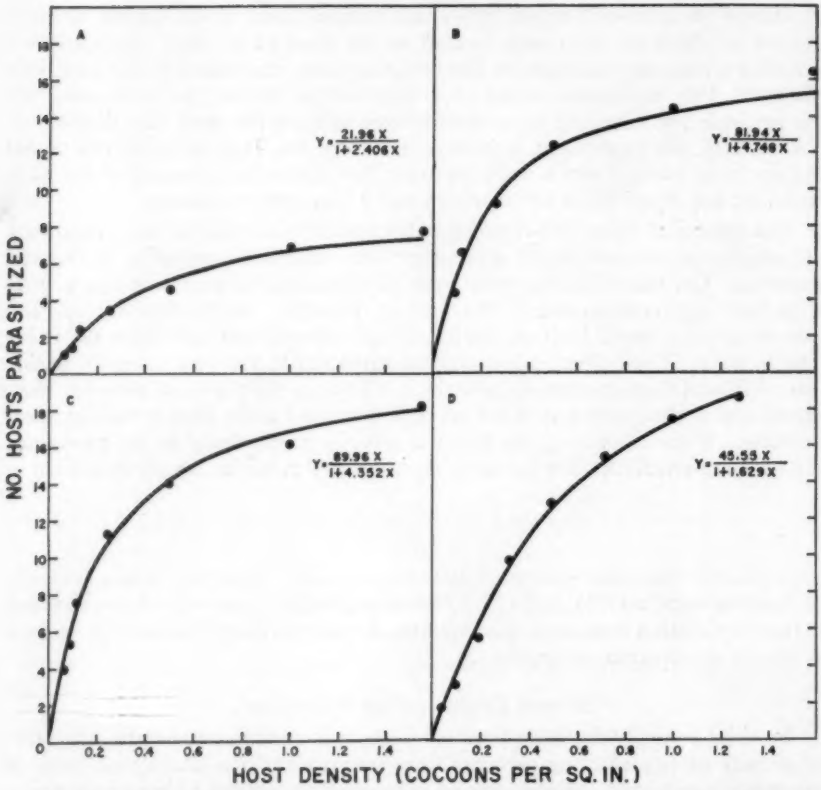

Fig. 4. Functional responses of *Dahlbominus fuliginosus* (Nees) searching for *Neodiprion sertifer* (Geoff.) cocoons in the laboratory. (Burnett, 1951).

A, B, and C: Experiments conducted at 16, 20 and 24°C respectively with different host densities achieved by changing the cage size.

D: Experiment conducted at 24°C with cage size constant.

basic equation (4) and it can be seen that it closely describes the data (P>99%). The data appearing in graphs A, B, and C represent different temperature conditions. The effect of these different temperatures was exerted through the constants *a*, the instantaneous rate of discovery, and *b*, the time spent in handling the hosts. Thus *a* increased from 0.9 to 3.4 to 3.7 as the temperature increased and *b* decreased from 2.6 to 1.4 to 1.2. Changing the area of search (Fig. 4D) modified the response mainly by decreasing *a* from 3.7 to 1.9. The value of *b* was only slightly changed, i.e. from 1.2 to 0.9.

The experiments conducted when the parasites searched for *Neodiprion sertifer* (Geoff.) cocoons distributed on a lawn (Burnett, 1954) are shown in Fig. 5, and again equation (4) can be seen to closely describe the observed points (P>99%). This equation fitted equally well when *Dahlbominus* was searching for *Neodiprion lecontei* (Fitch) cocoons distributed in a woodlot (Fig. 6A, P>99%) (Burnett, 1958). Thus it seems that the basic functional response equation describes with satisfactory accuracy the functional responses of *D. fuliginosus* searching for sawfly cocoons under a wide variety of conditions. The

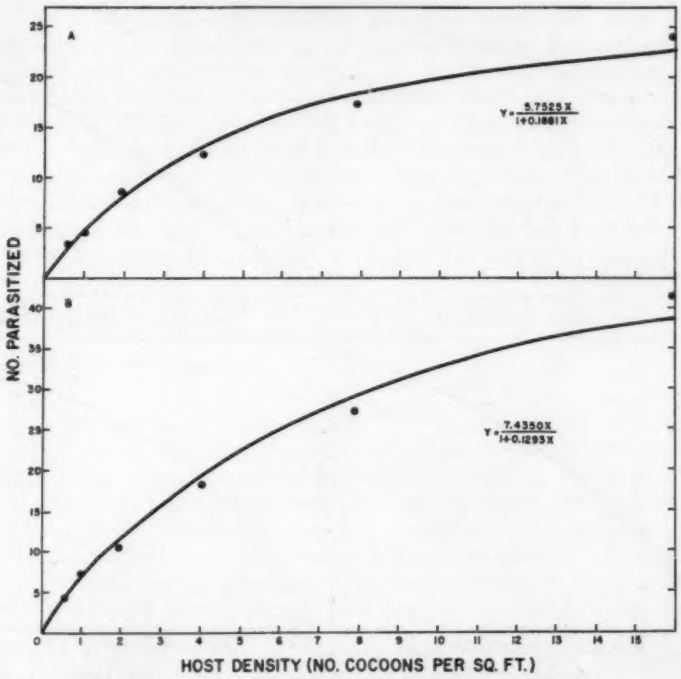

Fig. 5. Functional responses of *Dahlbominus fuliginosus* (Nees) searching for *Neodiprion sertifer* (Geoff.) cocoons on a lawn. (Burnett, 1954).
A: Temperature below 17.5°C.
B: Temperature 17.5°C to 24°C.

only differences in the responses under these different conditions are in the values of the instantaneous rates of discovery and in the time spent in non-searching activities.

Three other bodies of host-parasite data are available, and the next three figures represent the functional responses demonstrated by *Chelonus texanus* Cress. searching for eggs of *Anagasta kühniella* (Zell.) (Fig. 6B) (Ullyett, 1949a); by *Cryptus inornatus* Pratt searching for cocoons of the beet webworm *Loxostege sticticalis* (L.) (Fig. 6C) (Ullyett, 1949b); and by *Nasonia vitripennis* (Walker) searching for puparia of *Musca domestica* L. (Fig. 6D) (De Bach and Smith, 1941). Again equation (4) is seen to describe the data very well and even the poorest fit (Fig. 6D) is highly significant (P>95%).

Although the basic functional response equation is seen to describe with satisfactory accuracy a wide variety of responses obtained under a variety of conditions, it is still dangerous to suppose that it completely *explains* the responses of these parasites. In order to completely verify the equation the assumptions upon which it is based must be tested in each case just as they were tested for the disc experiments. If this were done it might well be found that additional assumptions need to be added in order to completely describe these responses. But even if this is true, the two time-consuming behaviours, searching and handling of prey, are involved just as they were in the basic functional response revealed in the first disc experiment.

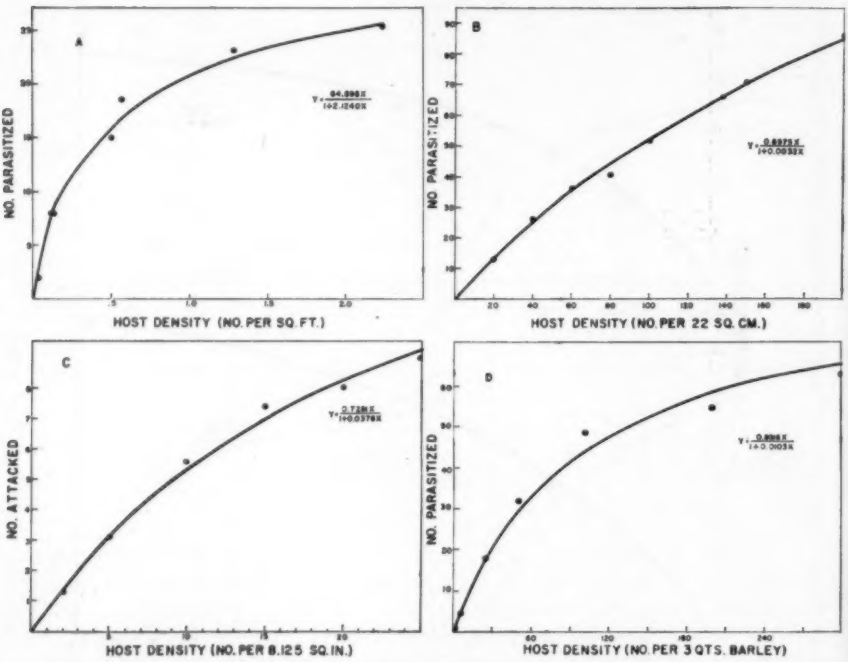

Fig. 6. A: Functional responses of *Dahlbominus fuliginosus* (Nees) searching for *Neodiprion lecontei* (Fitch) cocoons in a plantation. (Burnett, 1958).

B: Functional response of *Chelonus texanus* Cress. searching for eggs of *Anagasta kühniella* (Zell.) in the laboratory. (Ullyett, 1949a).

C: Functional response of *Cryptus inornatus* Pratt searching for cocoons of *Loxostege sticticalis* (L.) in the laboratory. (Ullyett, 1949b).

D: Functional response of *Nasonia vitripennis* (Walker) searching for puparia of *Musca domestica* L. (De Bach and Smith, 1941).

Other Mathematical Models

A number of equations have been proposed in the past to describe the effects of prey density upon the number of prey attacked. Many of these have been derived by transformation techniques and regression analyses, but since they provide no insight into mechanisms their value is limited. Moreover, a change of experimental conditions often requires a major change in the equation. Thus Burnett (1951) found that the functional responses of *D. fuliginosus* observed under laboratory conditions (see Fig. 4), could be described by a natural logarithm function of host density, whereas under semi-natural conditions (Burnett, 1954) (see Fig. 5) a square-root function had to be adopted. It has already been shown that equation (4) can apply in a wide variety of conditions simply by calculating the new values of the parameters.

Other equations have been proposed, however, by adopting certain simple and apparently reasonable assumptions. Lotka (1923) and Volterra (1926), for example, developed similar mathematical models to describe the change of prey or host density with time, and assumed, for this purpose, that the number attacked per predator was directly proportional to prey density. Nicholson and Bailey (1935) made the same assumption under the conditions of a constant predator

density. Such functional responses should appear as straight lines, rising indefinitely as prey density increases. The only functional responses that have been demonstrated with real animals however, are the S-shaped responses of small mammals and the responses of parasites which have continually decreasing slopes. Neither response is linear. Moreover it is difficult to imagine a situation where a predator's or parasite's attacks could increase indefinitely with increase of prey or host density; satiation or egg complement must impose an upper level for most predators and parasites, and even those predators that continue to kill after being satiated must reach an upper limit determined by the time required to kill. Thus the equations of Lotka, Volterra, and Nicholson and Bailey do not describe the facts.

Recently Watt (1959) has presented a more realistic equation to describe the effects of both prey and predator density upon the number of prey attacked. His equation is as follows:

$$N_A = PK\,(1 - e^{-aN_o P^{1-b}}) \qquad (11)$$

where N_A represent the number attacked, N_o the initial density of prey, P the number of predators searching, K the maximum number of attacks that can be made per predator and a a positive constant. This equation applies to a broader variety of conditions than the disc equation since the effects of predator density are included. When future experiments are conducted, the equations proposed here will be broadened to cover the same range of conditions. Now, however, equation (11) must be rewritten to permit comparison with the disc equation. This can be done by considering P as a constant so that PK, the maximum number of attacks that can be made by P predators, becomes a constant-K'. Similarly aP^{1-b} becomes a constant — a'. Equation (11), when predator density is constant, thus becomes

$$N_A = K'\,(1 - e^{-a'N_o})$$

or, by replacing N_A and N_o for the symbols employed in this paper, i.e. y and x respectively,

$$y = K'\,(1 - e^{-a'x}) \qquad (12)$$

In this form Watt's equation is identical to the one proposed by Gause (1934) and can be directly compared to those presented in this paper.

The basic assumption from which it is derived is that a given number of predators can generate a certain maximum number of attacks, K', and that the rate of attack is proportional "to still unutilized opportunity" (Gause 1934, P. 55) for attack. That is

$$\frac{dy}{dx} = a'\,(K' - y)$$

Watt applied his equation to the same parasite-host data that have been discussed in this paper, as well as to others in which the density of parasites varied, and found that his equation described the results with satisfactory accuracy. The basic functional response equation also provides an accurate description, even though it was derived from different assumptions. It is necessary, therefore, to examine the equations in detail to determine, if possible, which is the more acceptable.

In order to apply Watt's equation a value for K' must be calculated using the data available. When, as in the case of the parasite data, only y and x are measured, equation (12) is transformed to

$$\ln \frac{K'}{K' - y} = a'x \qquad (13)$$

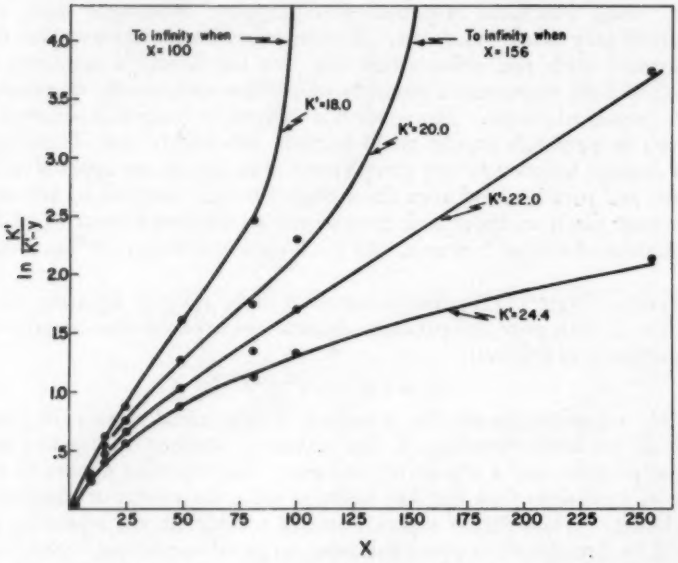

Fig. 7. Test of the fit of the equation $y = K' (1-e^{-a'x})$ to data obtained in the first disc experiment.

and values for K' are chosen by trial and error until a plot of $\ln \frac{K'}{K'-y}$ against x yields a straight line. This value is then chosen as the correct one, and the slope of the line provides the value for a'.

Since the first disc experiment provides a basic functional response from which all others are derived it was chosen as the first test of the validity of Watt's equation. More than y and x were measured in this experiment so that the true value of K' could be calculated without resorting to the indirect trial and error method. Since only two time-consuming behaviours were involved the maximum number of discs would be picked up (K') when all the available time was spent in picking up discs i.e. when

$$bK' = T_t$$

from which

$$K' = \frac{T_t}{b}$$

Thus in the first disc experiment K' should equal 1/0.0409 or 24.4. It can be seen from Fig. 7, however, that this value for K' yields a line with a decreasing slope. This is sufficient disproof of Watt's equation in this instance, but if the value for K' was not actually known, as in the case of the parasite data, lower values would have been assigned in an attempt to straighten the line. The effect of such lower values are also shown in Fig. 7. Dropping the value to 22.0 still does not straighten the line, and when it is lowered to 20.0 or less, the line bends towards infinity when $K'-y = 0$. All the data from the disc experiments and from five of the 10 sets of parasite data suggested this sort of relationship. In order to fit Watt's equation in these cases, K' was arbitrarily assigned the lowest value possible before the line began bending to infinity. In the disc experiments,

TABLE III.

Comparison of the Descriptive Value of the Disc and Watt's Equation.

Source of data		Sums of squares of deviations of observed from calculated values.	
		$Y = \frac{Ttax}{1 + abx}$	$Y = K'(1 - e^{-a'x})$
Disc experiment No. 1 (touch)		*0.9*	24.4
Disc experiment No. 2 (auditory)	(a)	*4.5*	23.1
	(b)	*3.5*	10.4
Dahlbominus fuliginosus (Nees) vs. *Neodiprion sertifer* (Geoff.) in the lab. (Burnett, 1951)	(a)	*0.6*	0.9
	(b)	*4.1*	7.8
	(c)	*0.7*	15.0
	(d)	1.1	*0.4*
D. fuliginosus vs. *N. sertifer over a lawn.* (Burnett, 1954)	(a)	*2.6*	5.7
	(b)	*6.5*	10.5
D. fuliginosus vs. *Neodiprion lecontei* (Fitch) in a plantation. (Burnett, 1958)		4.6	*3.1*
Chelonus texanus Cress. vs. *Anagasta kühniella* (Zell.) in the lab. (Ullyett, 1949b)		*14.0*	23.0
Cryptus inornatus Pratt vs. *Loxostege sticticalis* (L.) in the lab. (Ullyett, 1949b)		0.6	*0.3*
Nasonia vitripennis (Walker) vs. *Musca domestica* L. in the lab. (De Bach and Smith, 1941)		49.5	*26.5*

where the true value of K′ was known, this is of course inaccurate, but some arbitrary criterion had to be adopted in order to compare the two equations.

Table III compares the sums of the squares of the deviations of the observed number of attacks from the number calculated from each equation. The lower of each pair of values are underlined to indicate which equation best describes the data. Four of the 13 functional responses are better described by Watt's equation and nine by the disc equation. The mere fact, however, that the disc equation is more accurate in a wider variety of situations than Watt's equation is insufficient evidence, by itself, to discard the latter. Complete proof or disproof will only come when his basic assumptions are tested. Unfortunately such a test cannot be made with the parasite data since the true values of K' are not known. In the disc experiments, where the true values are known, Watt's equation is inaccurate. Since the functional responses demonstrated in these experiments are basic ones, it follows that Watt's equation is either inaccurate or at least incomplete in all situations.

Since the conflict between these two equations has arisen largely because of the different approaches adopted, it is appropriate, in closing, to contrast the two. Watt approached the problem by developing a number of sets of assumptions, that seemed reasonable on the basis of an intimate knowledge of the available literature. The equations derived from each set of assumptions were then tested against existing data and the one that described the greatest array was selected

as the proper one. Such an approach holds the promise of providing at least partial answers quickly, and this has considerable merit when so much biological information requires an analysis that will yield the insight into mechanisms that is necessary to suggest further work or practical control measures. There is, however, the danger that the selected equation will not provide an accurate *explanation* of the data in appropriate biological terms, even though it provides an adequate *description* of the data. Moreover, the approach tends to produce a restricted model, for there is no indication how models for more or less complex types of responses can be derived, nor indeed that other types exist.

The approach adopted in the present paper was different in that it began with the discovery of a *basic* functional response. That is, the only components operating were the ones that *had* to be present in all situations. All other components, that may be present in some situations and not in others, can be considered as subsidiary ones that can be analysed and incorporated after the basic response is fully explained. Thus the mathematical equation which incorporates the explanation of the basic response will evolve in logical steps along causal pathways that become progressively more complex. At any point along these pathways natural responses may be discovered, the explanation and description of which may be embodied by appropriate modifications of the basic equation. The approach also requires a proof that the equation accurately describes and explains the basic response, a proof that relies not only on the fitting of the equation to the data, but also on the testing of the basic assumptions by independently measuring the assumed constants. Hence the resulting mathematical models are accurate and are not restrictive.

Acknowledgments

I wish to acknowledge the considerable assistance rendered by Dr. R. M. Belyea and Mr. A. W. Ghent through discussion and criticism of the manuscript. I must also thank Miss Patricia Baic, whose 'predatory' behaviour provided data for the major portion of this paper.

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(Received May 7, 1959)

A Supernumerary Compound Eye in the Grasshopper *Eyprepocnemis plorans ornatipes* (Walker, 1870) (Orthoptera : Acrididae)

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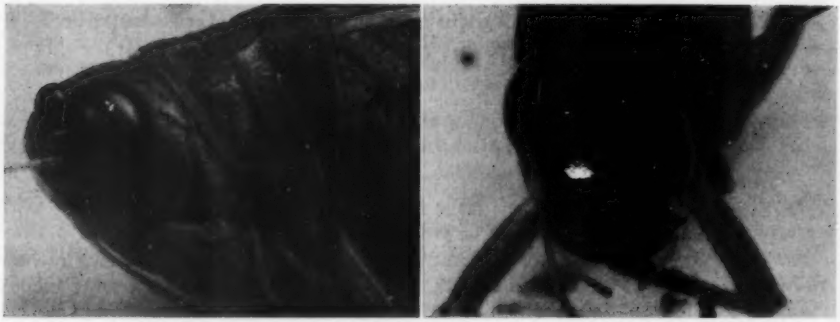
Whilst we were examining a large number of Acridoidea in connection with current morphological studies, an interesting specimen of *Eyprepocnemis plorans ornatipes* (Walker) came to our notice. The specimen, a female with three compound eyes, was discovered among many normal examples of the same species kindly provided for study from stock reared under artificial conditions at the Anti-Locust Research Centre, London, England.

Teratology in insect eyes has long been known, probably the earliest record being that of Stannius (1835), who described a worker honey-bee (*Apis mellifera* L.) in which the two compound eyes were completely fused into a single, symmetrical, transverse compound eye. Later Lucas (1868), Dittrich (1891) and Lotmar (1936) recorded further examples of cycloptic bees. Eyeless *Drosophila melanogaster* [auctt.] (Diptera) are, of course, well known. Frivaldszky (1886) stated that in a specimen of *Cerambyx scopolii* Füess. (Coleoptera) the left compound eye was replaced by an antenna, both antennae being on the left side, one in its usual place, the other behind it on the curved surface of the eye. In *Syrphus perplexus* Osburn (Diptera), Osburn (1908; 1910) noted a specimen in which the left compound eye was wanting, a third antenna, posterior to the normal one and arising from a fossa of its own, being present in its stead. Janda (1913) recorded a small antenna or antennae partially replacing an eye after its amputation in *Blatta orientalis* L. (Dictyoptera) and *Tenebrio molitor* L. (Coleoptera), and Krizenecky (1912; 1913a; 1913b) reported an antenna replacing an eye after amputation and removal of the optic ganglion in four specimens of the latter species. Bridges and Morgan (1919) mention examples of squat mutation of *Drosophila melanogaster* [auctt.] (Diptera), in which the eye often has a protruding lump caused by an extra antenna pushing partially or entirely through it.

It might not be inappropriate also to cite a few recorded cases of ocellar abnormalities. In the honey-bee Stannius (*op. cit.*) mentioned a reduction of the number of ocelli from three to one, and Lucas (*op. cit.*) recorded complete suppression of ocelli. In the Orthoptera, a specimen of *Melanoplus femur-rubrum* (DeG.) (Acrididae) with two median ocelli was described by Blackman (1912), and a specimen of *M. differentialis* (Thomas) with four median ocelli was recorded by Glasgow (1925).

Supernumerary compound eyes in insects have not commonly been reported, but several such records exist. Kiesenwetter (1873), for example, recorded a supernumerary eye set on a ring standing up above the centre of the head in *Vesperus luridus* Rossi (Coleoptera), Brûlerie (1875) reported a specimen of *Calathus fuscus* (F.) [*C. ambiguus* (Payk.)] (Coleoptera) with a small additional eye on the vertex, and Dohrn (1884) described a specimen of *Carabus nitens* L. (Coleoptera) with a supernumerary compound eye on the thorax. For orthopteroid insects, Cappe de Baillon (1927) figures specimens of *Carausius morosus* Br. v.W. (Phasmida) having two antennae and two eyes on each side of the head, or two antennae on each side and three eyes, the median eye being formed by fusion of supernumeraries belonging to each side, or with three eyes and three antennae, the third eye and antenna being median. He also gives a further



Figs. 1-2. *Eyprepocnemis plorans ornatipes* (Walker) ♀, showing development of supernumerary compound eye. 1. lateral; 2. frontal.

example of a double monster with an asymmetrically fused head having an extra eye and two antennae situated on the right side.

In the specimen of *Eyprepocnemis plorans ornatipes* (Walker) herein recorded, the extra compound eye is of the form illustrated in the accompanying photographs (Figs. 1 and 2). It is considerably smaller than the normal eyes and situated to the left of the frons, in front of, and very close to, the left compound eye which is itself slightly reduced in size. Like a normal eye, the supernumerary eye is surrounded by a well-marked suture produced internally to form a high skeletal ridge surrounding the ommatidia. Its facets are normal in shape and of the same size as those of the other two eyes. The three ocelli are also normal in shape and size, but the left lateral ocellus is situated just below the extra eye and is thus lower in position than the right. The other parts of the head and its appendages are quite normal in structure and position.

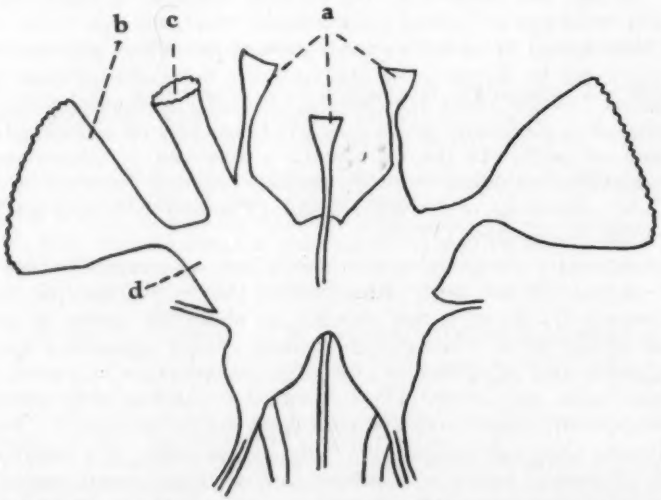


Fig. 3. Fore-brain and associated nerves of abnormal *Eyprepocnemis plorans ornatipes* (Walker) ♀. (a) Occellar ganglia and nerves; (b) optic ganglion; (c) supernumerary optic ganglion and nerve; (d) optic lobe.

The supernumerary eye was found to be innervated by its own optic ganglion and a long, thick, optic nerve, arising from the optic lobe as illustrated (Fig. 3). The left protocerebral lobe is partially fused with the left optic lobe. The other parts of the brain and the innervation of the ocelli were found to be normal. The presence of the nerve connection from the brain suggests that the extra eye was fully functional, but in our present state of knowledge it would seem profitless to speculate as to the cause of this abnormality.

Our thanks are due to Dr. F. O. Morrison for the photographs and to Dr. B. P. Uvarov, Director of the Anti-Locust Research Centre, London, for providing us with the material among which this abnormal specimen was discovered.

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(Received March 18, 1959)

A Method of Rearing Caddisflies (Trichoptera)

By GLENN B. WIGGINS[1]

In a number of the systematic studies of caddisflies with which I have been concerned, it has been necessary to rear larvae to the adult stage in the laboratory. Several methods proposed for rearing aquatic insects were considered, but these seemed open to some improvement, mainly because, for my purpose, it was necessary to rear large numbers of larvae in individual containers. For this reason the rearing equipment described here was designed. The principal advantage gained through its use is that relatively little maintenance is required to achieve fairly constant rearing conditions for large numbers of larvae, with each larva in a separate cage. By combining a number of individual cages into a unit, with its own supply of water and compressed air, attention to the needs of each individual cage is reduced considerably. By adding additional units, the capacity of the equipment can be doubled or trebled, while the corresponding increase in the maintenance requirements is proportionately much lower. In addition to providing an efficient means of rearing larvae in the laboratory, the same equipment can be used in the field under various conditions. Although caddisflies have been the only insects reared up to now, it is altogether likely that similar equipment would be suitable for other aquatic groups as well.

Design of the Apparatus

Essentially, the apparatus consists of a number of small rectangular cages, each constructed of aluminum screening, and suspended from a single wooden frame into a tank of flowing water (Figs. 1, 2). The number of cages on each frame and the dimensions of the cages may be altered to suit individual requirements. In my own apparatus, each frame held 24 cages, arranged in three rows, with the dimensions used for each cage shown in Fig. 4.

The Cages

The individual rearing cages are constructed from aluminum screening, 18 x 14 mesh, cut according to the pattern given in Fig. 4. Right-angled folds toward the inside are made along all of the broken lines, the two sides marked *a* being folded first, followed by those marked *b*. This ensures that the shorter flaps will be on the outside of the overlapping corners, leaving fewer rough edges on the inside of the cage. Right-angled folds toward the outside are made along the dotted lines to form a retaining lip around the top. The overlapping corners are stitched together with single strands of wire removed from a sheet of the same aluminum screening.

The Frame

The frame which supports the cages is constructed of ¾-inch-square pieces of wood, as shown in Fig. 3. The offset arrangement of the short crosspieces allows them to be nailed easily and more securely from both ends.

Assembly

When the cages are inserted into the openings in the frame, the right-angled lip around the top of each cage rests on the frame (Fig. 5a), and is fastened to it by means of a hand stapler. Wooden strips, one inch wide and ¼ inch thick, are then nailed tightly to the frame covering the lips of all of the cages (Fig. 5b). Finally, ⅜-inch-square strips are centred and nailed to the one-inch strips (Fig. 5c). The shallow well thus formed around the top of each cage holds a glass plate which serves as a removable cage top. With the dimensions of the cages suggested in Fig. 4, three-inch-square lantern slide cover glasses proved to be

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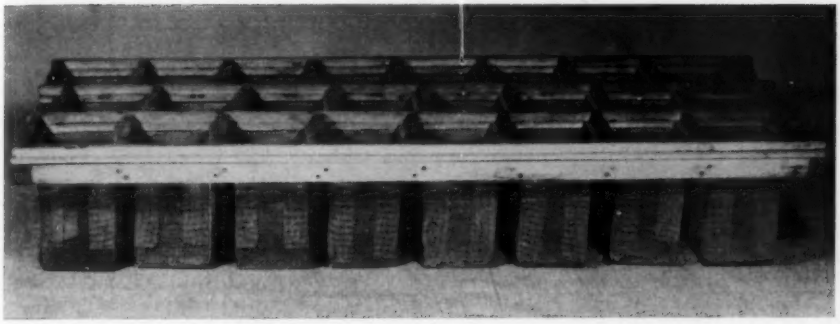


Fig. 1. Wooden frame with aluminum screen cages attached.

satisfactory cage tops. The frames around the individual cages are numbered consecutively with a metal punch, and the impression darkened with a soft lead pencil. Before use, and after every rearing season, all wooden parts are thoroughly saturated with raw linseed oil.

The Tank

The metal tank into which each frame of cages fits (Fig. 2) is about six inches deep and about three inches longer than the frame itself. Around the top of the tank is a ½-inch flange on which the two side pieces of the frame rest. A drain spout at one end of the tank maintains a constant level of water, and is so situated that the lower half of all cages is submerged, while the upper half is above the water level. This provides ample space for the newly emerged adult caddisfly. Extending the length of the tank three inches or so beyond the frame provides space for the inflow of water and for the installation of compressed air lines. When running water is being passed through the tanks, several of them may be arranged in a step-like series (Fig. 6) so that a single source of water and a single drain will serve for all of them.

Operation of the Apparatus

This apparatus can be used either in the laboratory or in the field. In the laboratory, the characteristics of various habitats with respect to temperature, dissolved oxygen and rate of flow can be simulated by adjusting the volume of water flowing through the tanks, along with the amount of compressed air

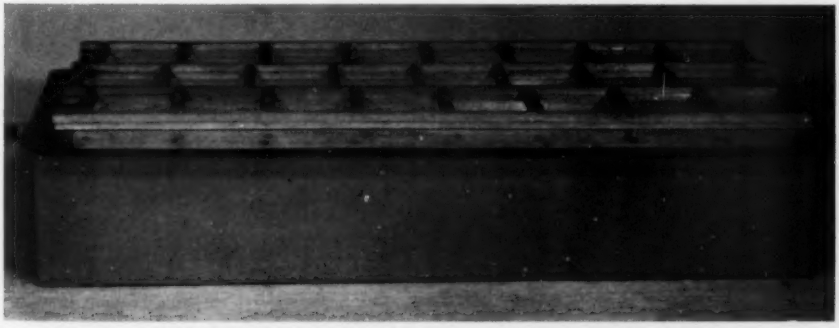
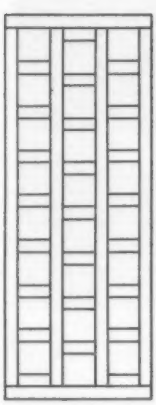


Fig. 2. Cages with glass covers in position in a metal tank.



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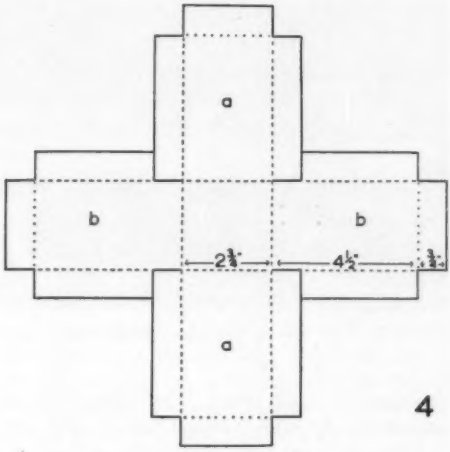

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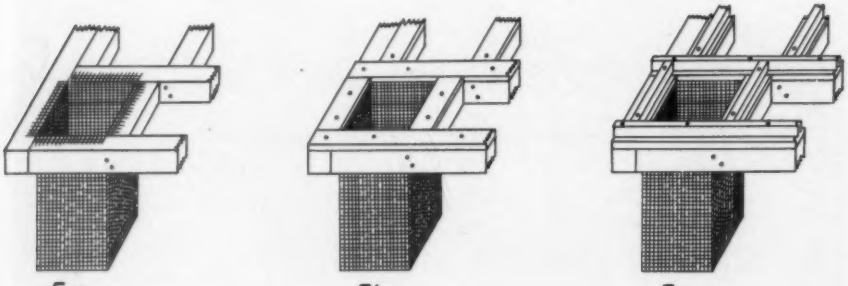
Figs. 3, 4. 3, plan of the wooden frame; 4, pattern for a wire screen cage.

released in the water. Passing tap water over a series of glass baffle plates before it enters the tanks will allow additional air to be dissolved in it, and will also help to allow harmful gases to escape. To provide space for such a baffle, the length of the frame of cages in the first tank of the series may be reduced. Streams of compressed air released into the water at each end of the tank at all times help to disperse any surface scum that may form on the water within each cage. In the field, the frame of cages may be set in the tank and water from a higher level passed through it. Alternatively, the frame may be removed from the tank and supported on a small raft-like structure, anchored and floating in an appropriate pond or stream, in such a way that the lower half of each cage is submerged.

Depending on the requirements of the species being reared, suitable materials are placed in each cage. For case-making caddisfly larvae appropriate materials such as leaves, sticks, or small pebbles are added. For species living in sand or mud, a small container, such as a Syracuse watch glass, containing the proper medium, may be placed on the bottom of each cage. A few leaves serve as food



5a 5b 5c

Fig. 5. Steps in fastening the cages to the frame.

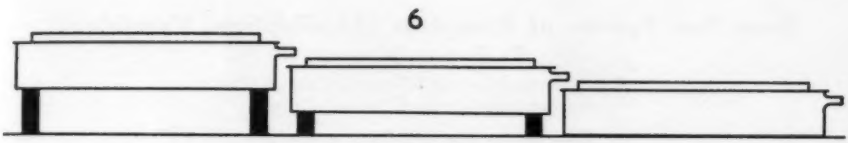


Fig. 6. Metal tanks and cages arranged in a step-like series.

for herbivorous species. Small organisms, such as enchytraeid worms, may be added for species requiring living animal food, but where this is necessary, it is well to have a small dish in the bottom of the cage to prevent the worms from escaping through the wire mesh before the insect can capture them.

To prevent the larvae from climbing up the screen sides and into other cages, it is important that the glass tops be in place at all times. Because most caddisfly larvae, including the normally herbivorous types, become cannibalistic when crowded under artificial conditions, it is best to keep each one in a separate cage. A number of pupae can, of course, be placed in a single cage. Following emergence from the pupa, the adult rests on or near the glass top where it is readily seen.

To date, larvae of the families Phryganeidae, Limnephilidae, Leptoceridae and Molannidae have been reared, and among these were species whose natural habitat ranges from cold spring streams to stagnant ponds. Larvae of the family Phryganeidae, which under natural conditions burrow into submerged logs, the banks of streams, or the bottoms of ponds, prior to pupation, have emerged successfully from pupal cases fastened to the sides of the screen cages or to a few dead leaves.

Summary

The design and operation of apparatus for rearing the larvae of caddisflies to the adult stage are described. The apparatus consists of a wooden frame to which rectangular, aluminum wire screen cages are fastened. The frame and cages are supported over a metal tank through which water is flowing, the lower half of each cage being submerged. A glass plate covers the top of each cage. Several tanks may be arranged in a step-like series in order that one source of water will serve for all of them. The same equipment can be used either in the field or in the laboratory.

(Received March 23, 1959)

Four New Species of *Evergestis* (Lepidoptera: Pyralidae)[1]

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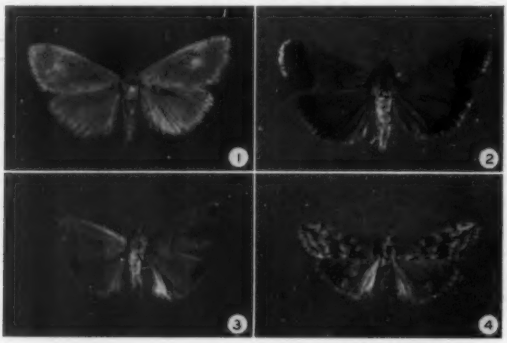
Entomology Division, Ottawa, Canada

Evergestis koepckei, new species

Figs. 1, 5

Female. Frons slightly produced, with a rudimentary median carina. Head, body and forewing above pale luteous, hind wing above and under side whitish. Abdomen above with narrow white basal band and with three or four obscure blackish-powdered mid-dorsal spots. Fore coxa, femur and tibia brown anteriorly. Forewing above with narrow, obscure, dark, irregularly dentate ante- and post-medial lines. Antemedial oblique outward to origin of Cu_1, then sharply angled and oblique inward to inner margin. Postmedial nearly parallel to outer margin, weakly indented along submedian fold. An hourglass-shaped mark at the end of the cell. All these markings surrounded by faint fulvous clouding. Outer margin with minute black dots at ends of veins. Fringe concolorous. Hind wing with one or two dark dots in submedian fold and with black terminal dots at the veins. Under side of forewing with lunate discocellular mark and anterior half of postmedial line conspicuously dark.

Female genitalia. Ovipositor densely pilose; apophyses short and slender; ductus bursae moderately constricted a little before ostium, with a sclerotized collar about three times as long as wide; bursa elongate, gradually broadening anteriorly, armed with a pair of large, reniform, heavily sclerotized and spinose signa, each situated on a spinulose disc.



Figs. 1-4. *Evergestis* spp. 1, *E. koepckei* Munroe; 2, *E. brunnea* Munroe; 3, *E. anticlina* Munroe; 4, *E. antofagastalis* Munroe.

Closest in appearance to *E. aridalis* Barnes and McDunnough (1914: 232), but larger and paler and differing in details of the markings.

Holotype, ♀, Hda. Taulis, ca. 6° 50′ S, 79° 10′ W, Peru, 20-30 Apr., 1954, H. Koepcke. In the Bavarian State Zoological Collection, Munich.

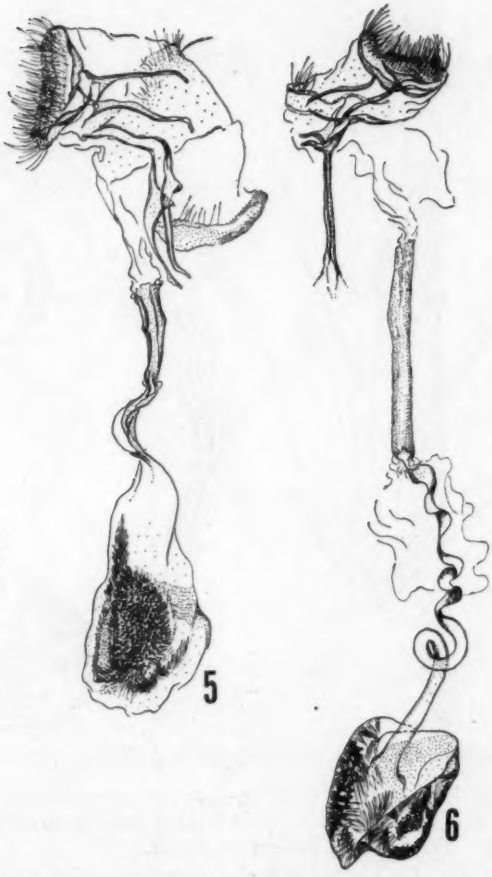
Paratype, ♀, same locality and collector, 1-10 May, 1954. No. 6764, Canadian National Collection.

Evergestis brunnea, new species

Figs. 2, 6

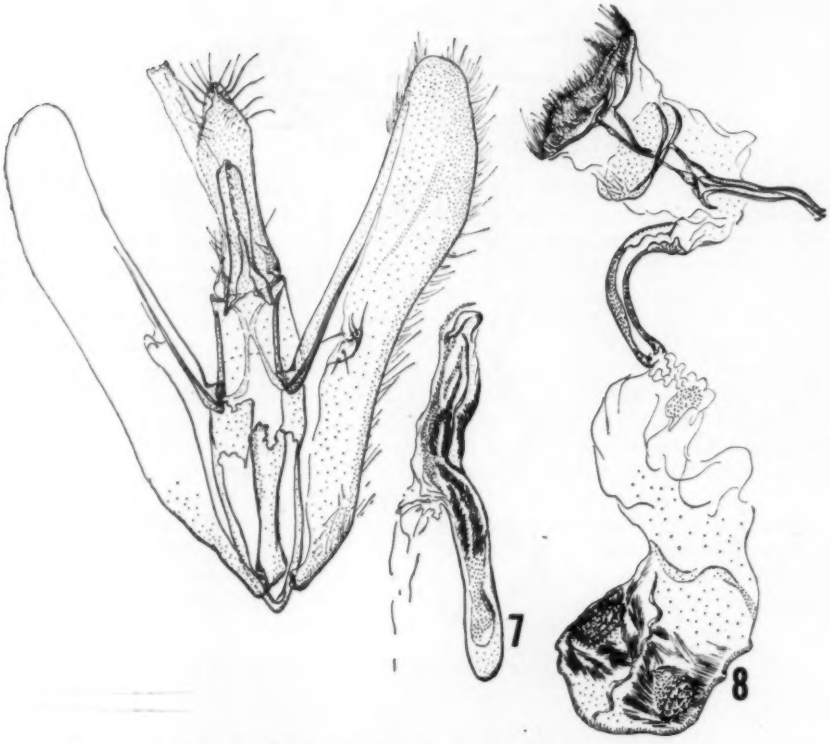
Female. Head, thorax, abdomen and forewing above faintly lustrous brown

[1]Contribution No. 3935, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.



Figs. 5, 6. *Evergestis* spp., ♀ genitalia. 5, *E. koepckei* Munroe; 6, *E. brunnea* Munroe.

with a violaceous tint, hind wing translucent fuscous, dark-bordered. Membrane of wings with a nacreous iridescence. Forewing with obscure dark sub-basal dots in and beyond cell. Antemedial line narrow, obscure, dark, arising about two-fifths of the way out costa, running obliquely to just above Cu, where it is produced, then incurved to another outward tooth on submedian fold, then incurved again to inner margin. Discocellular 8-shaped, the obscure dark outline being filled with ground colour. Postmedial weakly and irregularly sinuate, roughly parallel to outer margin, narrow, dark, obscure, followed by a narrow line of ground-colour, then the whole area to the termen dark, a little paler in the outer part. Traces of a subterminal row of dark dots, a terminal series of black dots on the veins, a series of black internervular dashes in the base of the fringe, and a dark brown line in the grey fringe. Hind wing mostly almost transparent fuscous, the veins dark; an opaque terminal region, fringes and terminal dots as on forewing. Body and wings beneath pale grey, forewing with a large, suffused, dark, lunate discocellular spot, with a white line along



Figs. 7, 8. *Evergestis anticlina* Munroe, genitalia. 7, ♂; 8, ♀.

vein, both fore and hind wings with indistinct dark postmedial line and subterminal shading. Termen and fringes as above.

Female genitalia. Ovipositor densely pilose; posterior apophyses short and weak; anterior ones somewhat longer and stronger; ductus bursae constricted before ostium to a slender, sclerotized tube, about ten times as long as wide; bursa elongate, with a large diverticulum from left side leading to ductus seminalis; two elongate-reniform, heavily sclerotized and spinose signa; corpus bursae finely spinulose.

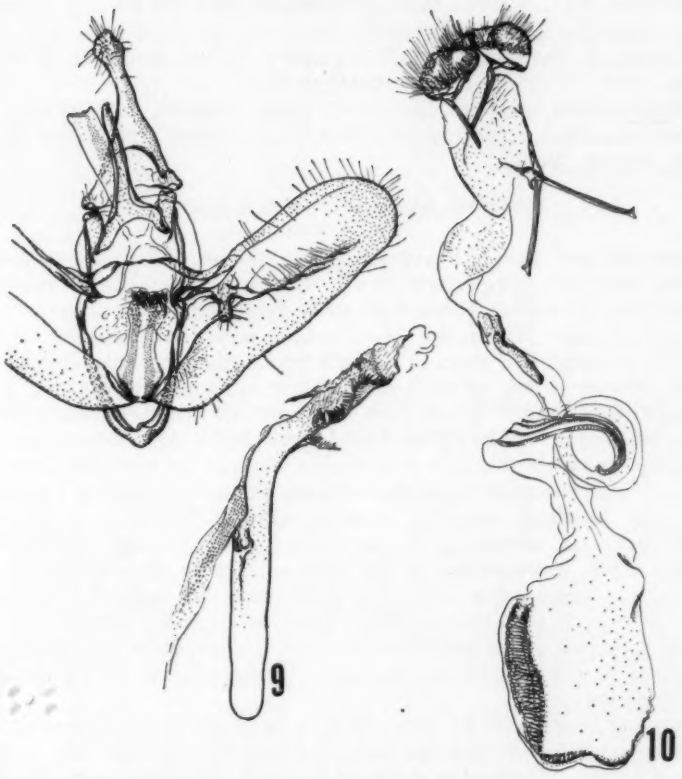
Somewhat similar in appearance to *Evergestis inglorialis* Hampson (1918: 183), but with forewings matt brown, with dentate antemedial line, and with hind wings infuscated.

Holotype, ♀, and paratype, ♀, Hda. Taulis, ca. 6° 50′S., 79° 10′W., Peru, May, 1954, H. Koepcke. Holotype in Bavarian State Zoological Collection, paratype No. 6765, Canadian National Collection.

Evergestis anticlina, new species

Figs. 3, 7, 8

Head and body above moderately pale olivaceous fuscous. Forewing with base and disc pale, area beyond postmedial line contrastingly dark. Antemedial line straight, sloping inward from costa at two-fifths to inner margin at one-third. A dark discocellular lunule, filled with the pale ground. Postmedial straight,



Figs, 9, 10. *Evergestis antofagastalis* Munroe, genitalia. 9, ♂; 10, ♀.

perpendicular to inner margin. Hind wing white, semitransparent, with a broad blackish terminal band, narrowing somewhat posteriorly. Under side pale with markings of upper side repeated but more faintly.

Male genitalia. Uncus rhomboidally dilated in distal part, dorsally setose towards tip; gnathos strong, dorsally toothed, about two-thirds length of uncus; tegumen broad, vinculum very narrow; juxta long and slender; valve long and slender, costa narrowly inflated, tip rounded; penis bent at middle, vesica minutely scobinate.

Female genitalia. Ovipositor densely pilose; posterior apophyses slender and weak; anterior apophyses longer and stronger, somewhat compressed; ductus bursae membranous for a short distance before ostium, then sclerotized to form a curved tube; bursa elongate, with a broad diverticulum leading to ductus seminalis; fundus with a pair of heavily sclerotized and spinose, ovate signa, surrounded by a pilose zone.

Similar in facies to *E. bilinealis* (Walker), new combination, = *Caprinia? bilinealis* Walker (1865: 1366) = *Lygropia bilinealis*, Hampson (1898: 729), but distinguished by having the transverse lines of the forewing anteriorly convergent, not parallel, and by having the discocellular marking much more conspicuous.

Holotype, ♀, C. Ceratia (Ctcs), Argentina, May 16, 1952, J. Foerster (ex coll. J. L. Sperry). Type no. 6726, C.N.C.

Allotype, ♂, Provincia Oran, N Argentina, 300 m., Jan., 1916, J. Steinbach, C.M.Acc. 5571. Type lot no. 117, Carnegie Mus.

Paratypes: five specimens in the Carnegie Museum, three in the C.N.C., from Provincia Oran, Argentina, and from Puerto Suarez, 150 m., and Provincia del Sara, 450 m., Bolivia.

Evergestis antofagastalis, new species

Figs. 4, 9, 10

Frons flat and oblique, head pale grey; thorax and abdomen pale grey, variegated with darker, especially above. Legs grey, tips of tibiae and of tarsal joints whitish. Forewing above light grey variegated with darker, the whole with a bluish cast. Antemedial line blackish, somewhat smudged, its general course at right angles to costa as far back as Cu, then strongly oblique inward to inner margin; strong outward points along principal veins giving a jagged appearance. Orbicular a diffuse grey lunule in cell, touching antemedial; reniform a rectangular or hourglass-shaped grey patch on discocellulars. Postmedial grey anteriorly, blackish posteriorly, followed by a whitish, then a grey, shade, somewhat irregular, strongly oblique, shallowly excurved opposite cell, then weakly incurved, touching posterior edge of reniform. A diffuse subterminal dark area, narrowing to costa, paler towards margin, followed by a dark then a pale terminal line; in the latter a series of black points at the end of the veins. Fringe white with grey streaks opposite ends of veins and with two distinct grey longitudinal lines. Hind wing above diffuse grey, with traces of dark postmedial and broad terminal bands; postmedial accentuated in cubital field, as are the dark terminal dots. Fringe whitish with a single longitudinal grey line.

Forewing beneath smoky grey, veins as far as postmedial obscurely darker. Antemedial smoky grey, obscure, obsolete anteriorly. Discocellular spot quadrate, smoky grey. Postmedial as above, but with pale zone much less distinct. Termen and fringe as above. Hind wing pale grey, with obscure discocellular dot and dentate postmedial band. Termen and fringe as above but paler.

Male genitalia. Uncus slender and spatulate, apex subacute; gnathos slender and tapering, weakly toothed above; tegumen moderately wide; vinculum narrow; juxta elongate, more strongly sclerotized laterally than medially; valve of moderate length, with costa narrowly inflated and tip rounded; a rounded, ventrally directed process from inner surface near base; penis sharply bent beyond middle, vesica finely scobinate.

Female genitalia. Ovipositor lobes rather narrow, strongly setose; apophyses weak; ductus bursae membranous, with a short sclerotized collar; bursa elongate, with a broad diverticulum leading to ductus seminalis; a pair of ovate, strongly sclerotized, spiny signa, each surrounded by a pilose zone.

This species rather closely resembles *E. simulatilis* (Grote, 1880: 94) from western North America, but has the wings narrower, the markings more diffuse, and the antemedial line of the forewing much less oblique.

Holotype, ♂, allotype, ♀, and 2 ♂, 10 ♀ paratypes from Paposo, Antofagasta, Chile, Sept., 1952, L. Peña. No. 6727, C.N.C.

Acknowledgments

I am indebted to Dr. Walter Forster, Bavarian State Zoological Collection, Munich, Germany, and Mr. Harry K. Clench, Carnegie Museum, Pittsburgh, Pa., for the loan and gift of material.

Summary

Four new neotropical species of *Evergestis* are described.

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(Received March 24, 1959)

Winter Rearing of Tent Caterpillars, *Malacosoma* spp. (Lepidoptera : Lasiocampidae)[1]

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During the winter of 1957-58 larvae of the tent caterpillars *Malacosoma pluviale* (Dyar) and *M. americanum* (F.) were reared to provide material for tests on the spore-forming bacterium reported by Bucher (1957). As there is little published information on winter rearing of tent caterpillars, except that of Sippell (1952) on *M. disstria* Hbn., the technique is given below.

At Belleville, eggs of *M. americanum* are laid in June. Embryonic development starts immediately and within a month the eggs contain fully formed larvae capable of movement. These unhatched larvae enter diapause and after exposure to winter temperatures emerge when the buds of their food trees break in the following spring. *M. pluviale* has a similar cycle in Western Canada.

To rear tent caterpillars during the winter two problems must be solved: breaking the diapause of the eggs and breaking the dormancy of tree buds. Both of these can be solved by cold treatment.

Breaking Diapause of Tent Caterpillar Eggs

Exposure to low temperatures before embryonic development was complete killed the eggs. The embryos matured in three to four weeks at 75°F. but were less resistant to cold than embryos six weeks old. Thus the eggs were not exposed to cold treatments until they were at least six weeks old.

Excessive desiccation before hatching also caused death. The foam surrounding the eggs protects them from drying at the sides and top and, in the field, the living bark on which the eggs are laid protects the lower surface. In the laboratory, where the egg masses were handled on short twig segments that soon died, the eggs dried from the lower surface unless held at a high humidity. A satisfactory humidity for both primary incubation of the embryos and subsequent cold treatment was 80 per cent. This was obtained in desiccators containing saturated aqueous solutions of ammonium sulphate with excess of the salt. Humidities close to 100 per cent promote mold growth on the twigs that may invade and destroy the eggs.

Tests were made to determine the minimum time at 25 ± 5°F. required to break diapause of eggs of *M. americanum* and *M. pluviale* laid in the laboratory

[1]Contribution No. 3906, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

TABLE I

Hatching of egg masses of *Malacosoma pluviale* and *M. americanum* after various periods of storage at 25± 5° F. and incubation at 75° F.

Weeks in storage	Days of incubation for		Percentage emergence of developed embryos
	First emergence	Peak emergence	
0	79	79	0–2
1	73	73	0–3
2	–	–	0
3	25–51	51–74	2–10
4	34–35	39–41	0–3
5	29	44	0–20
7	23–26	26–29	15–20
8	16–21	24–26	40–50
10	13–14	13–18	90–98
12	7	7	90–98
14	6	6	90–98
16–40*	5	5	90–98

*Data for 16 weeks storage and over, 30 egg masses; for other storage times, 2–4 masses.

and of *M. pluviale* collected in British Columbia. The results were pooled because eggs from all three sources showed no significant differences in behaviour. Each egg mass was handled separately on a short segment of twig placed in a sterile three-inch shell vial stoppered with a cotton plug. The eggs were incubated at 75°F. and 80 per cent relative humidity for six weeks or, for field-collected eggs, until the embryos were mature. Then they were exposed successively to 55 ± 5°F. and 45 ± 5°F. for two to three days each and to 35 ± 5°F. for 20 days, and finally stored at 25 ± 5°F. After various periods in storage, egg masses were incubated at 75°F. until the eggs hatched or dissection showed the embryos to be dead. During this secondary incubation a humidity close to 100 per cent was maintained by placing the eggs, still within the shell vials, in plastic boxes with moist filter paper. Diapause was considered broken when peak emergence from a single egg mass occurred within 24 hours of first emergence and when further cold storage did not greatly decrease the incubation time.

In tent caterpillars diapause cannot be considered an all-or-none state which can be terminated by a given exposure to cold. Both individual embryos of an egg mass and individual egg masses varied in the length of exposure required to break their diapause. A few embryos hatched after long periods of incubation following little or no exposure to cold. As the exposure time was prolonged, progressively greater numbers of embryos hatched after shorter periods of incubation (Table I). The diapause of all embryos was broken by 12 weeks exposure to 25°F. but an additional four weeks exposure reduced the time required for secondary incubation to five days. These results are in fair agreement with

data published for *M. americanum* by Flemion and Hartzell (1936) and for *M. disstria* by Hodson and Weinman (1945).

Six weeks of primary incubation, four of conditioning at progressively lower temperatures, 12 of cold storage, and one of secondary incubation gave a total of 23 weeks between oviposition and hatching. Thus eggs laid in June did not hatch before the middle of December.

Breaking Dormancy of Apple Leaf Buds

Both *M. pluviale* and *M. americanum* had previously been reared in the laboratory on apple leaves. As there was a greater supply of apple than of choke cherry or other food plants, experiments were conducted to determine a method of obtaining fresh apple leaves when needed.

On November 7, 1957, shortly after leaf fall at Belleville, hardwood cuttings with base diameters of one-half to one inch were taken from an abandoned apple orchard, wrapped in moisture-proof cellophane bags with wet cotton, and stored at 25 ± 5°F. On November 20, cuttings of smaller diameter from Siberian crab, *Malus baccata* (L.) Borkh., were obtained from Beaver Lodge, Alberta, and similarly stored. At intervals cuttings were removed from storage and incubated in wet vermiculite in a greenhouse at 75 ± 10°F. They were watered daily and the humidity of the greenhouse was kept as high as possible by wetting the floor. Beginning on February 4, 1958, cuttings were taken from apple trees in the field at intervals of three to seven days and incubated in the greenhouse without further cold treatment. Observations were made on the time required for the buds to burst and for the leaves to open to a size that could be used as larval food. This corresponded to the green cluster stage of bud development.

The buds of cuttings taken after leaf fall at Belleville and stored at 25°F. failed to develop unless they had been stored for six weeks. After six weeks storage only a small percentage of the buds burst and they required about four weeks incubation to reach the green cluster stage. As the storage period was increased more buds burst and developed faster. After 12 weeks storage the maximum number of buds burst and reached the green cluster stage after two weeks incubation.

According to the weather records, cuttings from Beaver Lodge had been exposed to about five weeks of freezing temperatures before collection. Some buds burst and reached the green cluster stage after three weeks incubation without further cold storage, but additional storage increased the percentage of bursting buds and hastened bud development. On cuttings stored for five weeks (a total of 10 weeks exposure to cold), a maximum number of buds burst after a week of incubation and reached the green cluster stage after two weeks.

Cuttings taken on February 4, 1958, at Belleville had been exposed to about nine weeks of temperatures below freezing in the field and produced buds in the green cluster stage after three weeks incubation. Maximum bud development occurred on cuttings taken near the end of February that had been exposed to about 12 weeks of freezing temperatures; the buds burst after one week of incubation and reached the green cluster stage a week later.

Thus from 10 to 12 weeks of exposure to freezing was required to break the dormancy of apple buds on cuttings and to ensure rapid and adequate bud and leaf development. Less than 10 weeks exposure resulted in lower percentages of bursting buds and slower leaf production; more than 13 weeks did not progressively shorten the bursting time. Cuttings stored artificially throughout this period generally produced leaves more slowly than those exposed to cold naturally on the trees.

Neither painting the cuttings with paraffin to reduce evaporation either before storage or before incubation nor scraping the bark at the bases of the cuttings to aid in water uptake hastened bursting of the buds.

As gibberellic acid was reported to break the dormancy of Elberta peach (Donoho and Walker, 1957), its effect on apple cuttings was tested. Cuttings were sprayed with 50, 200, or 500 parts per million of potassium gibberellate, or the buds were painted with 10,000 or 20,000 p.p.m. of potassium gibberellate or of gibberellin[2]. Gibberellic acid and gibberellin had no effect on the speed of leaf formation or on leaf size at any of these concentrations.

On all cuttings the leaves remained small and soft and failed to reach the mature size and texture of leaves formed in the field. If protected from burning in excessive sunlight, they remained fresh and satisfactory as food for over a week. The best leaves developed on hardwood cuttings with a minimum of flower buds. Cuttings with many flower buds produced small leaves. Cuttings from sucker growth produced few leaves of poor quality.

An unlimited supply of food leaves was available by the end of February from cuttings taken in the field at Belleville and incubated directly, but previous to this time food supply was limited by the number of cuttings in storage and by their production of buds. Cuttings taken on November 7 and artificially stored produced leaves satisfactory as food by the middle of January, 10 weeks after leaf fall (six weeks of storage plus four weeks of incubation), but only about 10 per cent of the buds burst, and food supply limited the number of larvae in rearing. By the middle of February, after 14 weeks (12 weeks of storage plus two weeks of incubation), stored cuttings produced leaves in abundance. As tent caterpillar eggs hatched by the middle of December, there was a period of one month when cuttings from an area with a climate like that of Belleville supplied no food and another month when food supply was critical. The cuttings from the colder region around Beaver Lodge provided food during this period.

Rearing Technique and Observations

When the eggs began to hatch, one or two apple leaves were placed in each vial containing an egg mass. A day or two later the larvae were removed to rearing containers. These were cylindrical pint cartons with two screened ports for ventilation and petri dish bottoms for lids. A bouquet of apple twigs in water in a vial was fixed to the bottom of the container with plasticene and the food was changed every two or three days. The larvae from a single mass were reared as a unit until the middle of the second instar and then divided into lots of 15 to 25 for further rearing. After the middle of the third instar, food consumption was too high to make bouquets practical and therefore fresh leaves were provided daily. The temperature of the rearing room varied from 75 to 80°F. and the relative humidity from 40 to 50 per cent.

Experimental larvae were tested individually and in groups. Group tests were made on larvae, reared as above, at any time after they reached the second instar. For individual tests, larvae were reared in three-inch shell vials and supplied with fresh food daily. As they display marked "follow-the-leader" behaviour (Wellington, 1957), they are difficult to rear individually, especially in the early instars. Thus individual larvae were not isolated before they had reached the middle of the third instar.

Throughout the rearing cycle the larvae from each egg mass were isolated

[2]The gibberellin was a product of Pfizer & Co., Brooklyn, N.Y. and contained a mixture of gibberellic acid and gibberellin A.

from those of other masses. Aseptic precautions were taken to avoid transmitting any disease from one container to another and particularly from one egg mass to another. Despite these precautions disease developed spontaneously among the larvae of some egg masses.

Larvae from egg masses laid in the laboratory by healthy females of *M. pluviale* or *M. americanum* did not become diseased, but the hatch from these egg masses was lower than from those laid in the field. This was due in part to a greater proportion of infertile eggs and in part to lowered vitality of the embryos.

Larvae were reared from 41 egg masses of *M. pluviale* collected in the field. In one lot of 17 masses from the Vancouver area, only two produced living larvae, none of which became diseased; the embryos of the other masses had matured but did not emerge, probably as the result of drying before arrival at the laboratory. Egg masses from three other areas in British Columbia hatched normally but a spontaneous virus disease developed in larvae from seven of 24 populations. The virus was the typical nuclear polyhedral virus well known in tent caterpillars and the insects died in the late second or early third instar, 14 to 18 days after hatching. As the incubation period of this virus is about seven days, it was presumably transmitted via the egg to a small number of larvae which spread the infection. The larvae of one egg mass from Cranbrook and of two egg masses from Nelson spontaneously developed the bacterial disease described by Bucher (1957). The external symptoms became evident when the larvae were about 18 days old and in the third instar but infection was light and some larvae escaped infection. The pattern of infection indicated that the disease was transmitted between the larvae of a single egg mass during the first or second instars before the mass was split into smaller lots of larvae and implicated the eggs as the source of the infection. It is most probable that a few spores were caught in the foam surrounding the egg mass and that a small number of larvae ingested these by chance as they emerged from the eggs and spread the infection throughout the group.

The larvae from healthy egg masses were used for experiments on transmission of the bacterial disease. From 90 to 95 per cent of the untreated control insects survived to form pupae and the remainder died from bacterial septicaemia or failure to molt. At 75°F. instars I and II each lasted about a week and cocoons were formed about four or five weeks after hatching.

Summary

Larvae of *Malacosoma pluviale* and *M. americanum* were reared during the winter by breaking the diapause of the eggs and the dormancy of food-tree buds. Twelve weeks exposure to a temperature of 25 ± 5° F. broke the diapause of both species. Optimum hatch occurred by the middle of December, 23 weeks after oviposition, an interval made up of six weeks of incubation to permit full development of the embryos, four weeks of conditioning at progressively lower temperatures, 12 weeks of storage at 25 ± 5°F., and one week of incubation. Food was obtained by forcing leaf buds on apple cuttings whose dormancy had been broken by 10 to 12 weeks of exposure to temperatures below freezing in cold storage or in the field. Maximum leaf development occurred on stored cuttings by the middle of February, 14 weeks after leaf drop in the Belleville area, but smaller quantities of leaves were produced a month earlier by reducing the storage time. Cuttings taken after natural exposure to cold on trees at Belleville produced numerous leaves by the end of February. Treatment of cuttings from Beaver Lodge, where leaf drop was earlier, provided food by the middle of December at a time when larvae were hatching in numbers. Disease did not

develop in progeny of healthy females reared in the laboratory, but larvae from some egg masses of *M. pluviale* collected in the field became spontaneously infected with a polyhedral virus and with a bacterial disease. Larvae from healthy colonies had a high survival under the methods of rearing.

Acknowledgments

I am indebted to officers of the Canada Experimental Farm at Beaver Lodge, Alta., for cuttings of Siberian crab and for current weather records, to several officers of the Forest Biology Division, Canada Department of Agriculture, for collections of eggs of *M. pluviale* in British Columbia, and to Mr. D. Farnsworth for technical assistance.

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(Received February 17, 1959)

Life-History and Habits of *Scolytus tsugae* (Swaine) (Coleoptera: Scolytidae) in the Interior of British Columbia[1]

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Introduction

Scolytus tsugae (Swaine) is a bark beetle that occurs throughout the Pacific Coast and Rocky Mountain Region and is common in the interior of British Columbia. Although Bedard (1938) reported that it had killed small areas of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) reproduction, it is of minor economic importance and usually confines its attack to tops, limbs, and logging slash. A knowledge of the life-history and habits of this insect is desirable for an understanding of the effects of interspecific competition on the development of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk., with which it is often associated in Douglas fir.

The study described in this paper was made during 1956, 1957, and the spring of 1958 near Lumby and Lac la Hache, B.C., at elevations of 2100 and 2800 feet, respectively. Gallery systems were tagged as the beetles initiated their attacks on three trees felled near Lumby in early July, 1956, and later examined at various ages for the presence of parents and progeny, gallery length, and larval mine length. These data were supplemented in 1957 and 1958 by observing additional material attacked by the beetles. All host material studied was Douglas fir unless otherwise indicated.

[1]Contribution No. 545, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

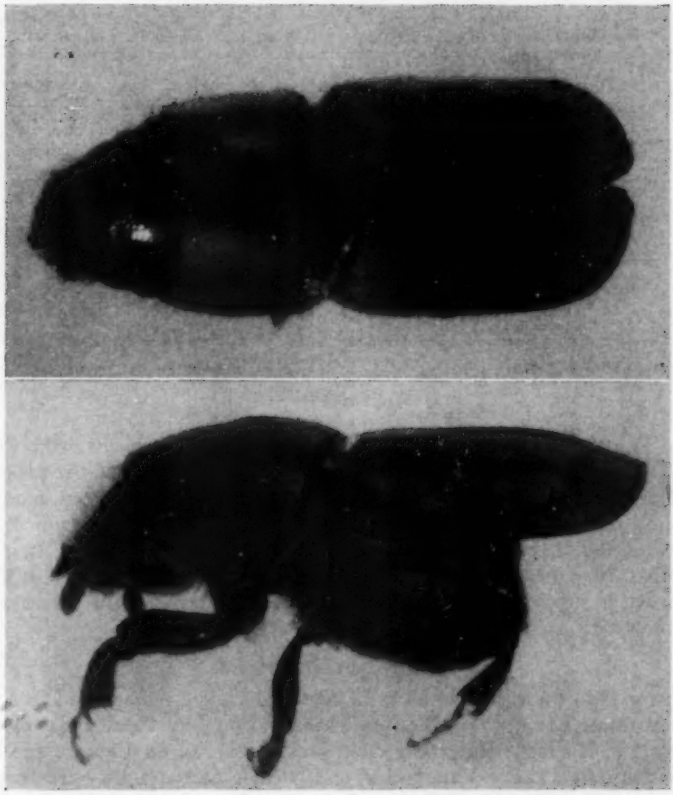

Fig. 1. Dorsal and lateral views of the adult of *S. tsugae*.

Description

The species (Fig. 1) was first described by Swaine in 1917. Due to the controversy over the validity of the generic name, much of the earlier literature refers to the group as the genus *Eccoptogaster*. Blackman clarified the issue in his revision of the genus in 1934. However, there is some doubt regarding the specific identification in that this species is very closely related to *Scolytus monticolae* (Swaine). Blackman states "This form (in reference to *S. monticolae*) is very closely allied to *Scolytus tsugae* and specimens assigned to *monticolae* are sometimes found in field series of *tsugae*. Also there are many intergradations between the more coarsely sculptured forms with the ventral abdomen opaque which are representative of *tsugae* and the more smoothly sculptured *monticolae* with the venter shining. The writer is somewhat at a loss in definitely assigning certain of these intermediate forms to either species." Hopping[2] believes that *tsugae* and *monticolae* comprise one variable species and that the name *tsugae* takes precedence.

Swaine (1917) described *S. tsugae* and *S. monticolae* as being 3.4 and 2.8 mm. in length, respectively, while Blackman stated that they are 2.7 to 3.4 and 2.2 to

[2]Hopping, G. R. In correspondence.

TABLE I

Data obtained from measurements of 110 adult *S. tsugae* in millimetres

Feature	Sex	Mean	C.L.[1]	s[2]	Range
Total length	♂	3.21	3.08–3.34	0.28	2.59–3.64
	♀	3.23	3.14–3.32	0.44	2.75–3.80
Length exclusive of head	♂	2.89	2.79–2.99	0.25	2.30–3.27
	♀	3.01	2.92–3.10	0.40	2.50–3.60
Width of prothorax	♂	1.13	1.09–1.17	0.08	0.97–1.25
	♀	1.14	1.11–1.17	0.12	0.73–1.33

[1]95 per cent confidence limits.
[2]Standard deviation.

2.8 mm. long, respectively, exclusive of head. In the present study the total length, the length exclusive of the head, and the widest part of the prothorax of 86 females and 24 males were measured. The beetles were sexed according to the method described by McMullen and Atkins (1956) for *Scolytus unispinosus* Leconte. A summary of the measurements is shown in Table I. It is worthy of note that these measurements lie between those given by Swaine and Blackman and indicate, in support of Hopping, that we are dealing with the group originally described as two species.

Life-History and Habits

During 1956 the earliest attacks of *Scolytus tsugae* were found in a recently burned area near Lavington (elevation 1400 feet) on July 10, whereas in 1957 and 1958 near Lac la Hache the first attacks were observed on June 28 and May 29, respectively. At Trinity Valley, during 1956, the first attacks were observed on July 14 on the top of a tree felled on June 29. On three trees felled on July 14, 1956, the first attacks were observed on July 16, with the peak attack occurring on July 19. The beetles continued to initiate galleries until August 29. No attacks occurred on trees felled at intervals of 15 days from May 15 to June 15 nor on trees felled on April 20. At Lac la Hache, in 1957, however, the beetles attacked Douglas-fir poles which were felled on May 6 and May 18 and four trees which had been girdled to the heartwood on May 17. In 1958, the attacks occurred largely on freshly felled material. In addition, in the spring of 1958, four pairs of window flight-traps similar to those described by Chapman and Kinghorn (1955) were used to sample flying insects in a forested area near Lac la Hache. These traps indicated that *S. tsugae* started flying on May 22, and continued until July 30 reaching their peak on June 17. This flight period greatly overlaps that of *S. unispinosus* making it necessary to check the identity of all the beetles captured. The pattern of the flying population is shown with the corresponding weather records in Fig. 2.

Although the majority of attacks occur in material which is 2.5 to seven inches in diameter with a bark thickness of 0.1 to 0.4 inches, we have recorded this species in material 13 inches in diameter with a bark thickness of 0.7 inches at densities up to 2.5 attacks per square foot. In the smaller material 20 attacks per square foot are common.

Scolytus tsugae are monogamous within their galleries, although there is

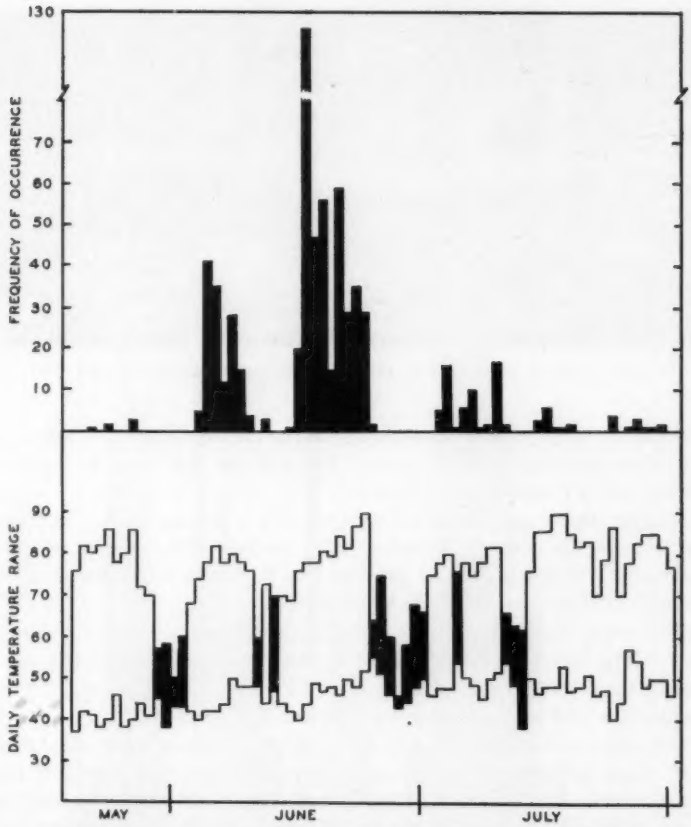

Fig. 2. Incidence of *S. tsugae* in flight traps with corresponding temperature data (black indicates days of heavy cloud or precipitation), Lac La Hache, B.C., 1958.

evidence (discussed later) that the males mate with more than one female, and the beetles work in pairs at least in the early stages of gallery construction. The entrance runs obliquely through the bark to the cambium where a small turning niche is cut. The female excavates the gallery (Fig. 3) longitudinally with the grain of the wood, in both directions from the turning niche, while the male remains in the entrance pushing out boring dust and presumably warding off intruders. The gallery is excavated at the cambial level, being approximately one-half in the wood and one-half in the bark. This feature readily distinguishes the gallery from that of *Pseudohylesinus nebulosus* (Leconte) which does not score the wood (Walters and McMullen, 1957). Also, the boring dust at the entrance to the gallery of *Scolytus tsugae* includes wood particles and thus has a whitish appearance, whereas that extruded by *P. nebulosus* is reddish.

The egg galleries of *S. tsugae* and *S. unispinosus*, which are very similar in appearance, can be separated on the basis of width; those of the former species are wider. An analysis of measurements of 50 gallery widths for each of the two species is presented in Table II.

Fig. 3. Gallery system of *S. tsugae* (larval mines darkened with ink).

The gallery of *S. tsugae* is constructed at the rate of about 0.15 inches per day; the rate decreases after 15 or 16 days. The average length of 135 galleries was 2.01 inches with a maximum of 3.6 inches.

The eggs, which are small (averaging 0.81 x 0.57 mm.), oval, and white, are laid singly in niches about 0.06 inches apart on both sides of the gallery. The average number of eggs laid in 62 galleries was 36.7 with a maximum of 76. The incubation period ranged from nine to 12 days.

Larvae were first observed on July 27, 1956, but were not common until August 1. The larvae mine for a short distance at right angles to the egg gallery and diverge towards the ends of the gallery (Fig. 3). The average length of 100 larval mines was 1.95 inches with a maximum of 3.1 inches

To determine the number of instars and the duration of stadia, larvae were collected from galleries of known age during the summer of 1956 and from galleries selected at random in mid-October, 1956, the spring of 1957 and the spring of 1958. Head-capsule widths of 1,843 larvae were measured with a calibrated ocular micrometer at a magnification of 100X to the nearest 0.014 mm. The ocular micrometer at 100X was too small to measure the larger specimens so an additional 569 were measured at 40X to the nearest 0.034 mm. A histogram of the frequency distribution of the head-capsule widths is presented in Fig. 4. The data were smoothed and analysed according to the method described by Forbes (1953). The frequency distribution and the analysis indicates four instars. Table III shows a summary of the head-capsule measurements.

To determine the durations of the stadia only those specimens whose head-capsule widths fell within the ranges of the means plus or minus their respective

TABLE II

Egg-gallery widths of *S. tsugae* and *S. unispinosus*

Species	Range in mm.	Mean in mm.	s	d.f.	t
S. tsugae	1.36–1.84	1.63	0.151	98	18.0000**
S. unispinosus	1.12–1.36	1.21	0.79		

**Significant at the 1 per cent level.

standard deviations were classified as to instar. The total number of each instar collected during the 1956 season was determined and the number of specimens of each instar collected at a given gallery age was recorded as a percentage of total for that instar. Then the accumulative percentage of each instar was plotted against gallery age; thus the difference in gallery age between successive instars at any given accumulative percentage should give the duration of the former

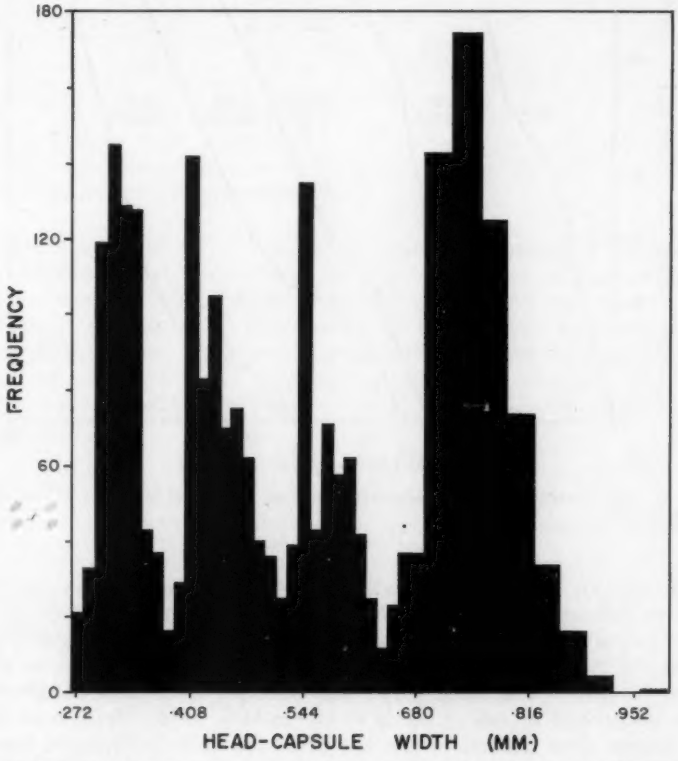

Fig. 4. Histogram of frequency distribution of 2,412 head-capsule widths of *S. tsugae*, Trinity Valley, B.C., 1956.

TABLE III

Head-capsule widths (mm.) of the larval instars of 2,412 *S. tsugae*, collected during 1956

Instar	Head-capsule width	
	Mean	Standard deviation
1	0.321	0.024
2	0.422	0.016
3	0.552	0.027
4	0.732	0.063

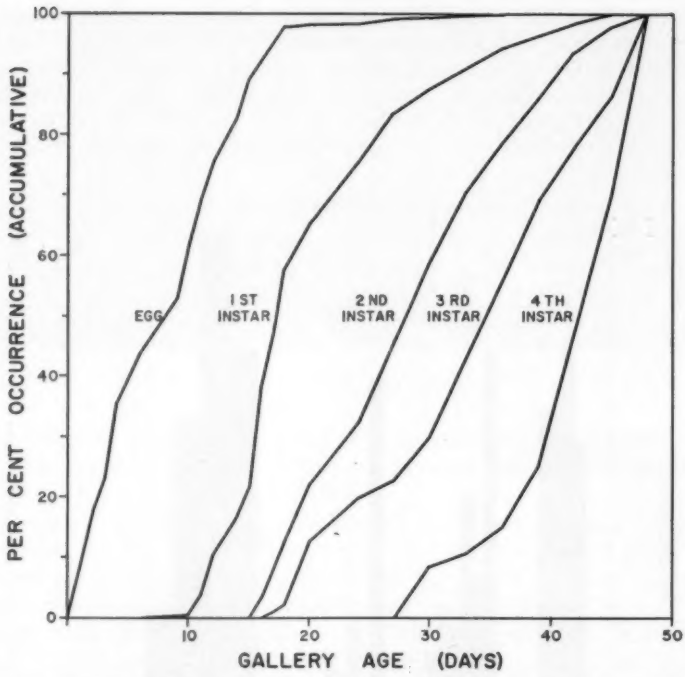

Fig. 5. Accumulative per cent occurrence of egg and larval stadia of *S. tsugae*, Trinity Valley, B.C., 1956.

stadium (Fig. 5). Average durations for the first two larval stadia and the pupal stadium as indicated at accumulative percentages in intervals of 10 from 20 to 80 per cent inclusive were used to arrive at the values presented in Table IV. Suitable data for the pupal stadium were not obtained during 1957 due to drying of the host material. The value given was obtained from data collected during the development of broods at Lac la Hache in May, 1958. Since both third and fourth instars were present in the last collection from galleries of known age in 1956, 100 per cent of each instar was reached at the same time. For this reason only those durations indicated by the four points from 20 to 50 per cent, inclusive, were used to determine the length of the third larval stadium. The instars which overwintered and their percentage occurrence, determined from collections on October 15, 1956, and April 15, 1957, were as follows: 2nd, 0.9 per cent; 3rd, 6.5 per cent; and 4th, 92.7 per cent.

The mean, mean maximum and mean minimum temperatures throughout the developmental periods are presented in Table V.

The fourth-instar larvae may pupate at the cambium-wood level or they may bore into the bark to complete their metamorphosis. In many cases they are found just beneath the scales of outer bark.

Table VI presents the disposition of the parents collected from galleries during 1956 and 1957. As is evident from this table, many of the beetles abandon their galleries. After the galleries were 16 to 20 days old, none contained more than one live parent. Nor do the number of dead parents account for all the

TABLE IV

Duration in days of the stadia of *S. tsugae*

Stadium	Duration	
	Mean	Range
Larval 1	8.1	7–9
2	5.6	4–6
3	9.3*	8–11*
4	overwinter	
Pupal	10.6	10–13

*Excluding the 6.5 per cent which overwintered.

missing ones. In an attempt to discover the fate of the parents which leave the galleries, infested material was placed in two cloth cages on August 1, 1956. Included in each cage were pieces of freshly cut Douglas fir, *Pinus contorta* Dougl., *Pinus ponderosa* Laws., *Pinus monticola* Dougl., *Picea engelmanni* Parry, and *Thuja plicata* Donn., along with approximately two inches of forest duff on the bottom of each cage. This material was examined in October, 1956, and in April, 1957, but no evidence was found of beetle activity outside of the originally infested material.

TABLE V

Mean weekly temperatures, in degrees Fahrenheit, during the development of *S. tsugae* at Trinity Valley, 1956, and Lac la Hache, 1958

Date	Mean	Mean max.	Mean min.
1956			
July 2–8	59.0	71.0	47.0
9–15	66.0	80.0	50.0
16–22	66.0	78.0	52.0
23–29	62.0	80.0	50.0
30–5	58.0	71.0	46.0
Aug. 6–12	60.5	75.0	47.0
13–19	63.5	79.5	48.0
20–26	64.5	78.0	51.0
27–2	56.0	69.0	45.0
Sept. 3– 9	50.0	65.0	35.5
1958			
April 21–27	36.0	47.0	24.0
28–4	49.0	62.0	31.0
May 5–11	49.5	64.0	35.0
12–18	48.0	66.0	30.5
19–25	60.0	79.5	40.5
26–1	54.0	67.0	41.0
June 2–8	59.0	74.5	43.0
9–15	58.0	71.0	45.5
16–22	64.0	80.0	48.0
23–29	58.0	68.0	49.0
30–6	61.0	74.0	49.0

TABLE VI

Disposition of parents of the 1956 brood in galleries of *S. tsugae*, Trinity Valley, B.C., 1956 and 1957

Gallery age (days)[1]	Number galleries examined	Per cent galleries containing				
		Living parents			Dead parents	
		2	1	0	2	1
1–10	72	88	9	3	0	2
11–20	75	46	46	8	0	7
21–30	20	0	63	37	10	10
31–40	15	0	70	30	10	10
41–50	15	0	65	35	0	20
Oct. 1956[2]	8	0	38	62	0	62
May 1957[2]	25	0	0	100	0	70
June 1957[2]	27	0	8	92	0	58

[1]For gallery systems of known age.
[2]Galleries selected at random.

It was noted that whenever only one of the parents was present it was usually the female. It is possible that the male's behaviour of remaining in the entrance hole to rid the gallery of boring dust is partially responsible for his loss to the family group. Perhaps this activity makes him vulnerable to predacious animals wandering over the logs. One feature which tends to substantiate this hypothesis is the fact that mutilated parents were frequently found in the entrance. However, there is evidence that not all the males are lost due to predation. Since males known to have taken part in gallery construction (with boring dust adhering to sternites of posterior ventral concavity) have been observed running over the bark, it is quite possible that the males are polygamous and wander from gallery to gallery mating with more than one female. This is believed to be the case with *Scolytus multistriatus* Marsh. (Hoffman, 1940) and may be supported for *Scolytus tsugae* by the fact that the sex ratio is four to three in favour of females during flight.

The life-history of *S. tsugae* is presented diagrammatically in Figure 6.

Scolytus tsugae has been reported from *Tsuga mertensiana* (Bong.) Carr., *Pinus monticola*, *Abies grandis* (Dougl.) Lindl., *Abies* spp. (Chamberlin, 1939), and *Tsuga heterophylla* (Raf.) Sarg.[3] as well as Douglas fir.

During the spring of 1958, an attempt was made to determine the host preference of this species. One section of Douglas fir, about two feet long and four inches in diameter, infested by *Scolytus tsugae* during 1957, was placed in each of four cloth cages. To each of the cages, freshly cut, three-foot sections of *Tsuga heterophylla*, *Pinus contorta*, *Pinus monticola*, *Pinus ponderosa*, *Juniperus scopulorum* Sarg., *Abies lasiocarpa* (Hook.) Nutt., *Picea engelmanni*, *Thuja plicata*, and *Larix occidentalis* Nutt., were added. In addition, Douglas fir was added to two of the four cages. The sections were examined after the beetles had emerged from the 1957 material and made their attacks on the fresh material. The resulting attacks are presented in Table VII.

Chamberlin (1939) pointed out that *S. monticolae* was the only species of *Scolytus* known to attack any species of *Pinus*, and suggested that *Pinus monticola*, from which the insect was collected, may have been an accidental host.

[3]Forest Insect Survey and Collection, Forest Biology Laboratories, Victoria and Vernon.

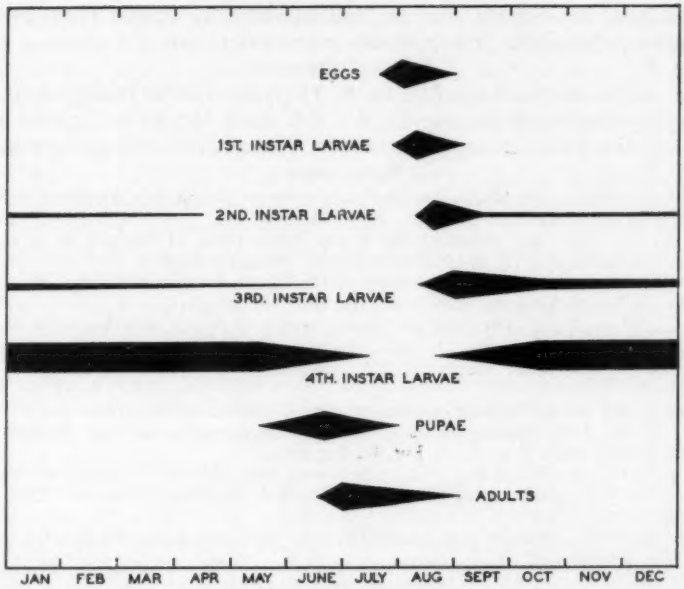

Fig. 6. Diagrammatic representation of life history of *S. tsugae* in the interior of British Columbia.

However, the results of this host preference study indicate that *Pinus monticola* is a true host of this group of *Scolytus*. In fact, the beetles seem to favour *P. monticola* along with *Tsuga heterophylla, Abies lasiocarpa* and *Larix occidentalis* as their hosts. The rejection of the Douglas fir may have been due to the pitchy condition of the material used.

Summary

The results of a study of the life history and habits of *Scolytus tsugae* (Swaine), made near Lumby and Lac la Hache, B.C., indicate that the beetle in the interior of the Province has a one-year life cycle with one brood per year. The beetle overwinters in the larval stage, chiefly in the fourth instar. Although

TABLE VII

Results of a cage study on the host preference of *S. tsugae* Swaine

Host species	Total area in sq. ft.	No. of attacks	Attacks per sq. ft.
Tsuga heterophylla	12.34	90	7.29
Pinus contorta	13.40	1(?)	0.07
Pinus monticola	12.61	149	11.02
Pinus ponderosa	11.80	1	0.09
Juniperus scopulorum	11.90	0	0.00
Abies lasiocarpa	11.88	28	2.35
Picea engelmanni	10.60	1 + 1(?)	0.19
Thuja plicata	11.80	0	0.00
Larix occidentalis	10.65	25	2.35
Pseudotsuga menziesii	5.35	10	1.86

(?)Not positively indentified as *S. tsugae*.

there has been some doubt that this species normally attacks *Pinus monticola*, cage studies indicate that it is probably a preferred host.

Acknowledgments

We would like to thank Mr. G. R. Hopping, Forest Biology Laboratory, Calgary, for identifying the insect. We also thank Mr. R. R. Lejeune and Mr. J. M. Kinghorn, Forest Biology Laboratory, Victoria, for reading the manuscript.

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Four Hymenoptera Newly Recorded As Parasites of the Armyworm, *Pseudaletia unipuncta* (Haw.) (Lepidoptera: Noctuidae)[1]

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At Ottawa, during studies on the parasites of the armyworm, *Pseudaletia unipuncta* (Haw.), in 1955, 1957, and 1958, 20 species of Hymenoptera were reared from larvae or pupae of the armyworm collected from fields in the area during July and August. Of the 15 species thus far identified, 12 were primary parasites; four of these, namely, *Euplectrus mellipes* Prov. (Eulophidae), *Hyposoter annulipes* (Cress.) (Ichneumonidae), *Microgaster auripes* Prov. (Braconidae), and *Therion sassacus* Vier. (Ichneumonidae), have not been previously recorded as parasites of *P. unipuncta*.

E. mellipes, an ectoparasite, was reared from six fourth-instar larvae of the armyworm in July, 1957, and from one in the third instar, four in the fourth, and one in the fifth in late July and August, 1958. Superparasitism always occurred, the number of parasite larvae per host ranging from five to 21 and averaging eight. The eggs of this species were laid in a mass on the dorsothoracic region of the host. The larvae fed gregariously on the immediate area where the eggs had been laid. As they increased in size their bodies formed a globular mass, the individual larvae being recognizable only by close examination. When fully grown, the parasite larvae dispersed over the body of the host, spun very loose cocoons, and transformed to pupae. The host larva became inactive as the parasite larvae neared maturity, and died about this time, its remains becoming enveloped by the parasite cocoons.

[1]Contribution No. 3939, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

In North America, this species has been recorded only from Ontario and Quebec, where it is known to parasitize *Feralia jocosa* (Guen.) (Noctuidae) and the larch casebearer, *Coleophora laricella* (Hbn.) (Coleophoridae) (Peck, 1951).

One specimen of *H. annulipes*, a solitary parasite, was reared from a fourth-instar larva of the armyworm in July, 1957. Schaffner and Griswold (1934) recorded this species in Maine and Massachusetts as a parasite of the noctuids *Catocala antinympha* (Hbn.), *Pyrrhia umbra* (Hufn.), and an unidentified species of *Catocala*. Townes and Townes (1951) listed a fourth host, the pistol casebearer, *Coleophora malivorella* Riley (Coleophoridae). The distribution of *H. annulipes* is transcontinental in Canada and in the Transition and Upper Austral zones in the United States (Townes and Townes, 1951).

Another solitary parasite, *M. auripes*, was reared from two fourth-instar larvae of the armyworm in July, 1957, and from one fourth-instar larva in July, 1958. This species has been reported as a parasite of the wheat head armyworm, *Faronta diffusa* (Wlk.) (Noctuidae) in the United States (Thompson, 1953). It has been recorded in Canada from Ontario, and in the United States from certain of the eastern states as far south as Kentucky, and west to Iowa and Kansas (Muesebeck and Walkley, 1951).

T. sassacus, also solitary in habit, emerged from a pupa of the armyworm in early August, 1955. The host pupa had formed from a sixth-instar larvae collected from a field of timothy in July. This species had already been recorded in Canada from Ontario and New Brunswick and it occurs in the eastern United States as far south as Virginia (Townes and Townes, 1951). Schaffner and Griswold (1934) reported it as a parasite of the fall webworm, *Hyphantria cunea* (Drury) (Arctiidae), and of *Cycnia inopinatus* (Hy. Edw.) (Arctiidae).

E. mellipes, *H. annulipes*, and *M. auripes* parasitized six and eight per cent of the armyworm larvae observed in 1957 and 1958, respectively. However, in the few infestations that were found near Ottawa, about 50 per cent of the larvae were already in the fifth or sixth instar; therefore, a higher record of parasitism by these three species would probably have been obtained had the armyworm populations been found at an earlier age. These three species are of particular interest because they destroy the larvae in the early instars before they can do much damage.

Acknowledgments

The author wishes to thank Mr. C. D. Miller, Dr. W. R. M. Mason, and Mr. G. S. Walley of the Entomology Division, Ottawa, for identifying the four species of parasites.

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(Received March 31, 1959)

Variation Between Samples of Immature Stages, and of Mortalities from Some Factors, of the Eye-Spotted Bud Moth, *Spilonota ocellana* (D. & S.) (Lepidoptera: Olethreutidae), and the Pistol Casebearer, *Coleophora serratella* (L.) (Lepidoptera: Coleophoridae), on Apple in Quebec[1]

By E. J. LeRoux[2] and C. Reimer[3]

In July, 1956, studies on mortality factors affecting abundance of immature stages of the eye-spotted bud moth, *Spilonota ocellana* (D. & S.), and the pistol casebearer, *Coleophora serratella* (L.), on apple were initiated in permanent orchard plots at Rougemont, Que. The object was to prepare life tables (Morris and Miller, 1954) for successive generations of each species through the rise and fall of a local epidemic. In preparing such tables, sound sampling techniques are necessary (Morris, 1955). This is a report on variation in samples, and in some mortality factors, of immature stages of the two species for the years 1956 to 1959, and on sampling recommendations.

The need for fundamental studies on populations of insect pests has been stressed by many workers (e.g., Uvarov, 1931; Thompson, 1939; Elton, 1946; Allee *et al.*, 1950). Recent reviews have stressed this need especially in the light of increasing use of pesticides for the control of crop and forest insect pests (Pickett *et al.*, 1946; Solomon, 1949, 1953; Ullyett, 1947, 1951; Clancy and Pollard, 1952; Morris and Miller, 1954; Glen, 1954; Massee, 1955; Neatby, 1955). Basic studies on factors determining abundance of crop and forest insect pests are few, some of the most notable having been carried out on the fall webworm, *Hyphantria cunea* (Drury) (Tothill, 1920, 1922); *Plutella maculipennis* (Curtis) (Ullyett, 1947); the knapweed gall-fly, *Urophora jaceana* (Hering) (Varley, 1947); the European corn borer, *Ostrinia nubilalis* (Hübner) (Stirrett, 1938); and the spruce budworm, *Choristoneura fumiferana* (Clem.) (Morris and Miller, 1954). None of these studies except that on *C. fumiferana* was a thorough study of mortality factors in development of a species from endemic to epidemic levels.

For fruit insects, specific factors known to be important in epidemiology have been investigated for various species (e.g., Lord, 1947; Stultz, 1950; MacPhee, 1953; MacPhee and Sandford, 1954; De Bach, 1949; Debach and Bartlett, 1951; DeBach *et al.*, 1953; Collyer, 1953; Collyer and Kirby, 1955; Pickett *et al.*, 1958). However, none of the studies has been intensive and detailed for factors that affect abundance of a major fruit insect pest.

Eye-spotted Bud Moth Status of the Pests

The eye-spotted bud moth, a major pest of apple in Quebec, was first reported from the province by Bethune (1891). Like many economic insects in North America, this species is of European origin (Porter, 1924). It is not continuously present in destructive numbers in fruit-growing regions of the province but occurs in periodic outbreaks. The rise and fall of an infestation usually covers a period of five years. The infestations may be local or widespread. In Quebec this species has one generation per year, the winter being passed as fifth-instar larvae in hibernacula. In late April or early May the larvae emerge to feed on the buds and developing leaves. In May and early June the larvae complete instars six and seven, making shelters in which they pupate in late June and early July. The adults emerge from early to mid July and lay eggs during the next

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two weeks. The larvae of the next generation develop to the fifth instar before hibernating.

Larvae in instars one to four skeletonize foliage from midsummer to early fall and scar the maturing fruit. Fifth-instar larvae, which overwinter in hibernacula near dormant buds, do not injure the tree in any way. Those of instars six and seven feed on developing buds and blossoms and only rarely on the newly formed fruit during May and early June. For all stages except overwintering larvae, the degree of injury varies with the larval density, the period of bloom, and the amount of the apple crop.

Pistol Casebearer

The pistol casebearer, a minor pest of apple in Quebec, was first reported from the province by Fletcher (1894, pp. 201-206). This species is of North American origin (Lintner, 1882). The pest, rarely observed in infestation proportions in apple orchards of the province (Maheux, 1924), is usually present at endemic levels only. The rise and fall of an infestation covers a period of approximately five years. The infestations may be local or widespread. In Quebec this species has one generation per year, the winter being passed as fifth-instar larvae in cases attached on or about dormant buds. In late April or early May the larvae move with their cases to the developing buds and there begin to feed. In May and early June they complete instars six and seven, and in late June they pupate within the cases. The majority of mature larvae stay on the tree to pupate; some move to the undercover. The adults emerge from early to mid July and lay eggs during the next two weeks. The first-instar larvae of the next generation build cases from leaves and excrement; the cases being retained throughout the larval period. Enlargement of the cases to accommodate each subsequent larger instar involves almost exclusively the use of leaves. The larvae develop to the fifth instar before hibernating in September.

The larvae of instars one to four feed on the leaves from midsummer to early fall, gnawing small holes on the surfaces or through the leaves eating as far as they can reach without leaving their cases. They move and repeat this process many times so that the leaves are covered with small pin-holes. The fifth-instar larvae, which overwinter in their cases on or about the dormant buds, do not injure the tree in any way. Those of instars six and seven feed on the swelling buds and the expanding leaves and flowers and only rarely on the newly formed fruit in May and early June. For all stages except overwintering larvae, the degree of injury varies with the larval density, the period of bloom, and the amount of the apple crop.

Experimental Plot

The experimental plot, Fig. 1, (hereinafter referred to as plot 'A') was in the Cistercian Fathers' apple orchard, Rougemont, Que. It consisted of 585 MacIntosh trees, covered an area of 12.7 acres, and was approximately 500 feet above sea level. It was bordered on the east and north by woodlands, and on the west and south by farm roads and commercial orchards. The trees were approximately 35 years old and in full production. Planted 35 feet apart, according to the hexagonal system of planting (Lewis, 1911), these were evenly distributed throughout the plot. The soil, which was of the Champlain terrace gravel type (Stobbe and McKibbin, 1937) and uniform throughout, offered good drainage and was typical of orchard soils of southwestern Quebec. Since clean cultivation was not practised, the orchard undercover was rich in number of plants; 160 species have been recorded to date. The plot was not subjected to

serious disturbances, except for mowing of the undercover once or twice a year and moderate pruning of trees each spring.

During the five years (1951 to 1955) preceding the period of study, the plot received a 'modified' spray schedule[4] for the control of arthropod pests. *S. ocellana* and *C. serratella* were present at endemic levels throughout this period. In 1956, a DDT spray was applied on June 12 for the control of a low-to-medium larval infestation of the fruit-tree leaf roller, *Archips argyrospilus* (Wlkr.). Counts taken after this application revealed the practical elimination of all beneficial arthropod species that prey on immature stages of the eye-spotted bud moth and the pistol casebearer. In July, a sudden upsurge of both pests were observed and the present study was initiated.

Throughout the study, insecticides were not applied to the experimental plot. Only the fungicide glyodin (2-heptadecyl-2-imidazoline acetate; Carbide and Carbon Chemicals Co., New York) was applied, for the control of apple scab.

Sampling Procedure

Sample Unit

The sample unit most suitable in the study of populations of *S. ocellana* and *C. serratella* and related mortality factors on MacIntosh apple trees is the leaf cluster. This unit of foliage, selected after the criteria of Morris (1955, Sec. 7), is relatively stable for mature MacIntosh trees and on it are found all immature stages of both species except winter larvae; these were sampled on cluster buds, on or about which they overwinter. The main number of leaf clusters per tree, for ten trees, was 11,300 $\pm$ 800, the mean number of leaves per cluster being 11.2 $\pm$ 0.2. The numbers of clusters per tree and of leaves per cluster did not vary significantly during the growing season (May to September) or from year to year, and did not appear to be influenced by growing conditions or by defoliation. The mean number of leaf clusters per tree did not vary significantly from the mean number of cluster buds (12,100 $\pm$ 600); this was expected since leaf clusters of the growing season give rise to cluster buds of the dormant season.

Sampling Procedure

To determine the distributions of the immature stages, and of mortality due to parasites, predators, diseases, and frost, of the two species within the crown of the tree, and to compare variation between trees with that within trees, the plot was divided into four equal blocks, L, M, N, and O (Fig. 1). Five trees selected at random were sampled per block. Each tree crown was divided horizontally into halves, designated A, the top, and B, the bottom. Each half was divided into four equal quadrants, N, S, E, and W, according to the four cardinal points of the compass. This provided for eight sampling sections within the tree crown, namely, NA, SA, etc. From each section 25 leaf clusters were collected and examined for immature stages and related mortality factors and data obtained were subjected to an analysis of variance.

Timing of Samples

In Quebec, the immature stages of *S. ocellana* and *C. serratella* develop simultaneously on apple. Estimates of densities of each stage and related mortality factors for both species were therefore obtained concurrently by direct sampling (i.e., the insects themselves, whether parasitized, killed by predators, diseased, or frozen, or insect signs were found and counted). For each species, five age intervals were assessed, namely, eggs, summer larvae (larvae hatching in July and

[4]Only pesticides known to be relatively innocuous to the natural enemies of apple pests were used.

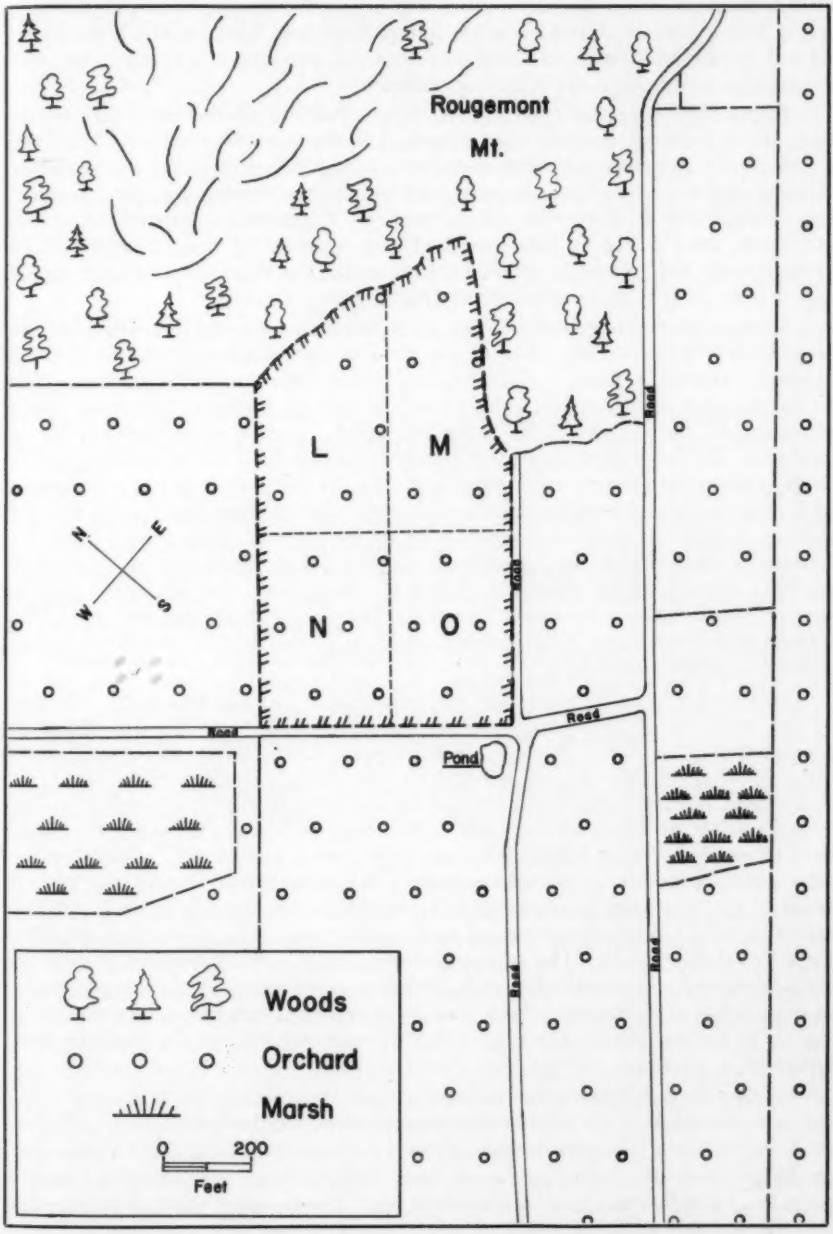

Fig. 1. Diagrammatic view of experimental plot 'A' with mountain and commercial orchard plantations nearby, Cistercians' apple orchard, Rougemont, Que.

present on the foliage till late September; instars one to four), winter larvae (larvae hibernating on the wood from late September to late April; instar five), spring larvae (overwintered larvae on foliage from late April to mid June; instars six and seven), and pupae. During each interval, sampling was carried out when the number in the stage was relatively stable.

Eggs.—Eggs were sampled in mid July. Because of the small size of the eggs, the leaf-cluster samples were examined in the laboratory under a binocular microscope. Eggs were classed as normal, parasitized, and killed by predators. Normal eggs for *S. ocellana* are pearly white with the developing embryo showing through; for *C. serratella*, opaque orange. Parasitized eggs of both species are black; those killed by predators had been emptied of their contents. Loss of eggs in the field through weather action, and in the laboratory through handling, was so small as to be obscured by the sampling error.

Summer Larvae.—Summer larvae were sampled from early August to mid September. Counts were made in the field by visual examination of the leaf clusters. Webbing, frass, and skeletonized leaves provided excellent visual clues to the presence of *S. ocellana* larvae; pin-hole damage to leaves and small, black, pistol-shaped cases, clues to *C. serratella* larvae. Larvae were not lost in examination of foliage since they were well concealed in their shelters and not prone to drop when the clusters were disturbed. During the period of study, reduction of summer larvae of both species through the action of mortality factors was not evident, except for newly-emerged larvae of the 1958-59 generation (Table IV, summer larval shelters, 1st sampling). Of the latter, those that were emptied of their contents were classed as 'killed by predators'. For all other summer larval counts, mean larvae per 25-cluster samples at hatching did not differ significantly from those at hibernation. Larvae in the samples that were normal reacted violently to probing.

Winter Larvae.—Winter larvae were sampled in October and April. Because of the small size of the winter shelters on bud clusters, twigs were examined in the laboratory under a binocular microscope. In October all larvae in the samples were normal. In late winter and early spring larvae counted were, for *S. ocellana*, normal, killed by frost, and by disease; and for *C. serratella*, normal. *S. ocellana* larvae killed by frost are dark brown or black, shrivelled, and either hard or nearly so; those killed by disease, light brown and flaccid. Counts revealed a great reduction in the number of *C. serratella* larvae during the 1957-58 winter; this was largely attributable to predation by birds (Table V, winter larvae, killed). Although cases on bud clusters are small, they are sufficiently large to attract birds. The overwintering larvae were abundant during the 1957-58 winter and provided a ready source of food for birds that overwintered in the neighbouring woods. Both the larvae and their cases were removed from the twigs by the birds. Predation by birds was not evident for overwintering larvae of *S. ocellana*.

Spring Larvae.—Spring larvae were sampled from early May to early June. Counts were made in the field by visual examination of the leaf clusters. Shelters of dying leaves tied together with silken threads provided excellent visual clues to the presence of *S. ocellana* larvae; large, well-defined, pistol-shaped cases on perforated leaves, clues to *C. serratella* larvae. Larvae were not lost in examination of the foliage since those of both species were well concealed in their shelters and were not prone to drop when the clusters were disturbed. Larvae present in the samples were normal. Mortality of *S. ocellana* attributable to predation by birds during the spring of 1958 (Table IV, spring larval shelters,

TABLE I

Analysis of variance of egg counts of *S. ocellana*, 1957-58 population (TABLE IV, eggs, total)

Source of variation	Expected mean square[1]	d.f.	Observed mean square	F
Between trees				
Blocks	$\sigma^2_e+8\sigma^2_t+40\sigma^2_b$	3	92.4	1.39
Trees within blocks	$\sigma^2_e+8\sigma^2_t$	16	66.4	3.00[2]
Within trees				
Levels	$\sigma^2_e+80\sigma^2_l$	1	547.6	24.78[2]
Quadrants	$\sigma^2_e+40\sigma^2_q$	3	12.0	
LxQ	$\sigma^2_e+20\sigma^2_{lq}$	3	21.7	
Residual	σ^2_e	133	22.1	

[1]σ^2_e, σ^2_t, etc., are population parameters; s^2_e, s^2_t, in the text are estimates of these parameters.
[2]Significant at the one per cent level.

not occupied) was assessed on the basis of the condition of the unoccupied shelters. Shelters attacked by birds had a perforated, shredded appearance and were empty. Predation by birds was not evident for *C. serratella* during the spring. For each species, evidence of mortality due to arthropod predators and parasites was not observed.

Pupae.—Pupae were sampled in mid June. Counts were made in the field by visual examination of the leaf clusters. Since both *S. ocellana* and *C. serratella* pupate in their larval shelters, visual clues for pupae were the same as for those of spring larvae. Pupae present in the samples were normal. Visual clues to predation of *S. ocellana* by birds (Table IV, pupal shelters, not occupied) were the same as for spring larvae. Predation of *C. serratella* by birds was not evident. For each species, evidence of mortality due to arthropod predators and parasites was not observed.

Methods of Statistical Analysis

An analysis of variance was made of all the counts without transformation. Insect counts are transformed in various instances, the object being to make the variance independent of density and to satisfy the additive property; both are conditions of the analysis of variance model. However, in the estimation of population parameters the transformation of the data can give rise to special problems, and it is time consuming as well. It is therefore advisable to analyse the data directly whenever these conditions are not seriously violated. In the present study, the density range was considered to be sufficiently low for direct analysis. For individual samplings, the inter-tree range of densities was less than twentyfold with a few exceptions, notably egg counts of *C. serratella* of the 1958-59 generation, for which the tree totals ranged from zero to 62 for upper side of leaves, and zero to 79 for total eggs (Table V, 1st sampling).

The analysis of variance is illustrated in Table I with one of the sets of data. The procedure for obtaining the expected mean squares may be found in a number of statistical books (e.g., Bennett and Franklin, 1954, Secs. 7.53, 7.62, 7.63). Since the expected values are based on the assumption, among others, that

the effects of trees, crown levels, etc., on densities and mortalities are additive, they can only be regarded as approximations. They are tabulated here to indicate how each component of variance can be tested for significance and how an estimate of it can be calculated.

All the mean squares except that for blocks have only one component of variance in addition to the intra-tree error variance σ_s^2; the latter is therefore the appropriate denominator in all their F ratios. As the mean square for blocks contains inter-tree error variance, σ_t^2, as well as σ_s^2, its F ratio has the mean square for trees in the denominator, i.e., F = 92.4/66.4 = 1.39, which has 3 and 16 degrees of freedom and is not significant.

Sources of Variation

In consideration of the reliability of a statistical estimate, a distinction must be made between two concepts that for convenience have been called *accuracy* and *precision*. Accuracy in this special sense denotes the absence of bias, which stems from *systematic* errors. Precision is a measure of the reproducibility of an estimate; it is concerned with *random* errors. Clearly, an estimate can rate high in accuracy and low in precision, and vice versa. In the mathematical model from which the expected mean squares (Table I) are deduced, differences between blocks, between crown levels, and between quadrants are regarded as systematic errors, and differences between trees and between clusters as random errors. The effect of random errors on the estimate of mean density can be controlled by the amount of sampling, i.e., by the number of trees and the number of clusters per tree that are examined. The effect of systematic errors can be eliminated only by taking the samples in such a way that all gradients of density, e.g., between crown levels, are represented in the sample in proportion to the amount of foliage.

All density differences reported in this section were statistically significant unless otherwise stated.

S. ocellana.—There were differences between blocks (Table II) in the numbers of spring larvae (2nd sampling) and winter larvae (1st sampling, total; killed by frost) in the 1956-57 generation; of eggs (upper sides of leaves), summer larval shelters (3rd, 5th samplings), spring larval shelters (1st sampling, clusters with blossoms; total), and pupal shelters (in prepupal stage; occupied; not occupied; total; on clusters with fruit) in the 1957-58 generation; and of eggs (1st and 2nd samplings, upper and lower sides of leaves; killed by predators), summer larval shelters (1st sampling, occupied), and winter larvae in hibernacula (1st sampling, total; killed by frost) in the 1958-59 generation. Egg totals for upper and lower sides of the leaves combined did not differ between blocks except for 2nd sampling, 1958-59 generation. No consistent pattern was observed in the differences between blocks.

Trees differed markedly in density for all stages except winter larvae and pupae of the 1956-57 generation, eggs (lower sides of leaves; parasitized), summer larval shelters (5th sampling), spring larval shelters (1st sampling), and pupal shelters (in pupal stage; on clusters without fruit) of the 1957-58 generation, and eggs (1st sampling, lower sides of leaves; parasitized, lower sides of leaves: 2nd sampling, lower sides of leaves; total; killed by predators upper and lower sides of leaves, total), summer larval shelters (1st sampling, live larvae; killed by predators), and winter larvae in hibernacula (1st sampling, total; killed by frost) of the 1958-59 generation; for these no tree differences were indicated. Although egg density for the 1957-58 generation (total) varied from tree to tree, the number of parasitized eggs did not. The percentage of eggs parasitized

TABLE II

Significance of variation due to blocks, trees, levels, quadrants, levels x quadrants, between samples of immature stages of *S. ocellana* in three generations, a sample of 25 leaf or bud clusters being taken from each of eight sections from each of 20 trees

Generation and stage	Blocks	Trees	Levels (Ratio A/B)	Quadrants	LxQ
1956-57 Generation					
Winter larvae, in hibernacula					
1st sampling, early April '57 occupied					
Total	x[1]	—	—	—	—
Killed by frost	x	—	—	—	—
2nd sampling, October '57[3] killed by frost	—	—	—	—	—
Spring larval shelters					
1st sampling, late April during movement to leaf clusters, occupied	—	—	—	—	—
2nd sampling, early May, occupied	x	xx[2]	6.2xx	—	—
Pupal shelters, mid June, occupied	—	—	—	—	—
1957-58 Generation					
Eggs, mid July					
Upper sides of leaves	xx	xx	1.4xx	—	—
Lower sides of leaves	—	—	1.9xx	—	—
Total	—	xx	1.5xx	—	—
Parasitized	—	—	1.4xx	xx	—
Summer larval shelters					
1st sampling, late July, occupied	—	xx	—	—	—
2nd sampling, early August, occupied	—	xx	—	—	x
3rd sampling, mid August, not all occupied	x	xx	—	—	xx
4th sampling, late August, not all occupied	—	xx	—	—	—
5th sampling, early September not all occupied	xx	—	1.5xx	x	xx
Winter larvae, in hibernacula					
1st sampling, October, occupied	—	xx	1.8xx	—	—
2nd sampling, early April, occupied					
Total	—	xx	1.5xx	—	—
Killed by frost	—	—	—	—	—
Killed by disease	—	—	—	—	—
Spring larval shelters					
1st sampling, early May during movement to leaf clusters, occupied					
On clusters with blossoms	x	—	1.4xx	—	—
On clusters without blossoms	—	—	—	—	—
Total	x	—	1.4x	—	—
2nd sampling, late May, not all occupied					
On clusters with fruit, occupied	—	x	1.5xx	—	—
On clusters without fruit, occupied	—	xx	—	—	—
Occupied	—	x	1.5xx	—	—
Not occupied[4]	—	—	—	x	—
Total	—	x	1.5xx	—	—
Pupal shelters, mid June, not all occupied					
In pupal stage	—	—	5.0x	—	—
Spring larval shelters (Cont'd)					
In pre-pupal stage	xx	xx	—	x	—
Occupied	xx	xx	1.3x	—	x
Not occupied[4]	x	xx	1.7xx	—	—
Total	xx	xx	1.5xx	x	—
On clusters with fruit, not all occupied	xx	xx	1.5xx	x	—
On clusters without fruit, not all occupied	—	—	—	—	—

TABLE II (*continued*)

Generation and stage	Blocks	Trees	Levels (Ratio A/B)	Quadrants	LxQ
1958-59 Generation					
Eggs					
1st sampling, mid July					
Upper sides of leaves	x	xx	—	—	—
Lower sides of leaves	xx	—	1.6xx	—	—
Total	x	xx	1.3xx	—	—
Parasitized, upper sides of leaves	—	xx	1.5x	—	—
Parasitized, lower sides of leaves	—	—	1.5xx	—	—
Total	—	xx	1.8xx	—	—
Killed by predators, upper sides of leaves	—	xx	—	—	—
Killed by predators, lower sides of leaves	xx	xx	—	—	—
Total	—	xx	—	—	—
2nd sampling, early September					
Upper sides of leaves	x	xx	—	—	—
Lower sides of leaves	xx	—	—	—	—
Total	xx	—	—	—	—
Parasitized, upper sides of leaves	—	xx	—	x	—
Parasitized, lower sides of leaves	—	xx	—	—	—
Total	—	xx	—	x	—
Killed by predators, upper sides of leaves	—	—	—	—	—
Killed by predators, lower sides of leaves	—	—	—	—	—
Total	—	—	—	—	—
Summer larval shelters					
1st sampling, late July, not all occupied					
Live larvae	—	—	—	—	—
Killed by predators	—	—	0.3xx	—	xx
Occupied	xx	xx	0.8xx	—	—
Not occupied	—	x	2.1xx	—	—
Total	—	xx	—	—	—
2nd sampling, mid August, not all occupied					
Occupied	—	xx	—	—	—
Not occupied	—	xx	—	—	—
Total	—	xx	—	—	—
3rd sampling, early September, not all occupied					
Occupied	—	xx	1.9xx	—	xx
Not occupied	—	xx	—	xx	xx
Total	—	xx	1.2xx	xx	xx
Winter larvae, in hibernacula, occupied					
1st sampling, October occupied					
Total	x	—	—	—	—
Killed by frost[5]	xx	—	—	—	—

[1]Significant at the 5 per cent level; dashes indicate non-significance.

[2]Significant at the 1 per cent level.

[3]Larvae killed by frost winter of 1956–57 still on trees.

[4]Mortality largely attributable to predation by birds, see text, section, *Timing of Samples* (winter larvae; spring larvae)

[5]Larvae killed by frost winters of 1956–57, 1957–58, combined, still on trees.

would therefore be expected to vary between trees, and an analysis of percentages (number of parasitized eggs/total number of eggs) confirmed this. For the 1958-59 generation, tree to tree variation was not observed for egg density, 1st sampling, and total parasitized eggs, 1st and 2nd samplings. Percentage mortality of spring larvae and of pupae attributable to predation by birds did not differ between trees although prey densities did.

Densities (except for 1st sampling, 1958-59 generation, killed by predators (0.3), occupied (0.8)) were consistently greater in the upper than in the lower

crown level, the ratios ranging from 1.3 to 6.2. Percentage mortality of spring larvae attributable to predation by birds was the same for the two crown levels although prey density was 50 per cent greater in the upper level. Percentage mortality of pupae due to birds, calculated separately, was greater in the upper crown by 26 per cent.

Differences between quadrants occurred in the 1957-58 generation in number of eggs parasitized, summer larval shelters (5th sampling), spring larval shelters (2nd sampling, not occupied), and pupal shelters (in pre-pupal stage; total; on clusters with fruit, not all occupied); and in the 1958-59 generation in numbers of eggs parasitized (2nd sampling, upper sides of leaves; total) and summer larval shelters (3rd sampling, not occupied; total). An interaction between quadrants and levels occurred for summer larval shelters (2nd, 3rd, 5th samplings) and pupal shelters (occupied) in the 1957-58 generation, and summer larval shelters (1st sampling, killed by predators; 3rd sampling, occupied; not occupied; total) in the 1958-59 generation.

Egg counts for upper sides of leaves (Table IV) averaged twice as high as those for the undersides in the 1957-58 generation, but did not differ significantly in the 1958-59 generation.

Analysis of all counts of summer larval shelters (Table IV) indicated that the total number of shelters increased progressively from 3.8 per 25-cluster sample in early August to 9.1 in late September for the 1957-58 generation, but showed only a slight increase from 8.2 in late July to 10.6 in early September for the 1958-59 generation. Larval density, for the 1957-58 generation, as estimated from occupied shelters (3.8) and later from hibernacula (3.3, 3.8) did not decline demonstrably from hatching to hibernation. Total number of larval shelters (8.2) and larval density (7.3), for the 1958-59 generation did not vary appreciably from hatching to hibernation (9.4). On April 29, 63 $\pm$ 8 per cent of the spring larvae of the 1956-57 generation had moved to leaf clusters; on May 14, 62 $\pm$ 3 per cent of the 1957-58 generation had similarly moved.

The distributions of percentage winter mortality of the 1956-57 generation (winter larvae, 1st sampling), percentage parasitism of eggs and percentage mortalities of spring larvae and pupae attributable to predation by birds, 1957-58 generation, were examined further by testing the observed variances against the binomial variance. These tests indicated that percentage mortalities due to frost and to predation by birds were each uniform between as well as within trees except for pupal mortality, which, as mentioned earlier, was greater in the upper than in the lower crown level. Though percentage parasitism of eggs was uniform within trees, between trees it decreased progressively with increasing host density, i.e., the chance of an individual being attacked decreased as host density increased.

C. serratella.—No differences between blocks (Table III) were found except for eggs (upper sides of leaves), spring larvae, and pupae in the 1957-58 generation, and eggs (upper and lower sides of leaves, 1st and 2nd samplings; parasitized, 2nd sampling; killed by predators, total, 1st and 2nd samplings), summer larvae (1st and 3rd samplings), and winter larvae in the 1958-59 generation. Inter-tree differences were pronounced at all stages except for spring larvae (on clusters with blossoms; total), and pupae (on clusters without fruit) in the 1957-58 generation, and eggs (upper and lower sides of leaves, 2nd sampling; total, 2nd sampling; parasitized, 1st and 2nd samplings; killed by predators, total, 1st and 2nd samplings) and summer larvae (3rd sampling) in the 1958-59 generation.

TABLE III

Significance of variation due to blocks, trees, levels, quadrants, levels x quadrants, between samples of immature stages of *C. serratella* in three generations, a sample of 25 leaf or bud clusters being taken from each of eight sections from each of 20 trees

Generation and stage	Blocks	Trees	Levels (Ratio A/B)	Quadrants	LxQ
1956-57 Generation					
Spring larvae					
1st sampling, early May	—	xx[1]	2.5xx	x[2]	—
2nd sampling, early June, migrated to ground cover	x	xx	6.2xx	—	—
Pupae, mid June	—	xx	—	—	—
1957-58 Generation					
Eggs, mid July					
Upper sides of leaves	x	xx	1.4xx	—	—
Lower sides of leaves	—	xx	1.5xx	—	—
Total	—	xx	1.4xx	—	—
Killed by predators	—	xx	—	—	—
Summer larvae					
1st sampling, late July	—	xx	—	—	—
2nd sampling, early August	—	xx	1.2xx	x	x
3rd sampling, mid August	—	xx	1.3xx	—	—
4th sampling, late September during movement to cluster buds	—	xx	1.6xx	—	—
Winter larvae					
1st sampling, October	—	xx	1.4xx	x	—
2nd sampling, early April	—	xx	0.8xx	—	x
Killed[3]	—	xx	1.5xx	—	—
Spring larvae					
1st sampling, early May	x	xx	—	—	—
2nd sampling, late May					
On clusters with blossoms	xx	—	—	—	—
On clusters without blossoms	x	xx	1.7xx	x	—
Total	xx	—	—	—	—
Pupae, mid June					
On clusters with fruit	—	xx	—	—	—
On clusters without fruit	xx	—	—	—	—
Total	x	xx	—	x	—
Migrated to ground cover	xx	—	—	—	—
1958-59 Generation					
Eggs					
1st sampling, mid July					
Upper sides of leaves	xx	xx	1.5xx	—	—
Lower sides of leaves	xx	xx	1.4xx	—	—
Total	xx	xx	1.5xx	—	—
Parasitized	—	—	—	—	—
Killed by predators, upper sides of leaves	—	xx	3.4xx	—	—
Killed by predators, lower sides of leaves	—	—	—	—	—
Total	xx	—	3.3xx	—	—
2nd sampling, early September					
Upper sides of leaves	xx	—	—	—	—
Lower sides of leaves	x	—	—	—	—
Total	xx	—	—	—	—
Parasitized	xx	—	—	—	—
Killed by predators, upper sides of leaves	xx	xx	—	—	—
Killed by predators, lower sides of leaves	—	—	—	—	—
Total	xx	xx	—	—	—
Summer larvae					
1st sampling, late July	xx	xx	1.4xx	—	—
2nd sampling, early August	—	x	1.2xx	—	—
3rd sampling, late August	x	—	—	—	—
4th sampling, mid September	—	xx	1.3xx	—	—
Winter larvae					
1st sampling, October	x	xx	1.3xx	—	—

[1]Significance at the 1 per cent level; dashes indicate non-significance.
[2]Significant at the 5 per cent level.
[3]Mortality largely attributable to predation by birds, see text, section, *Timing of Samples* (winter larvae)

Densities were consistently higher for the upper than for the lower crown level except for pupae, for which no difference was found, and winter larvae (2nd sampling), which were denser in the lower crown level, in the 1957-58 generation, and eggs (2nd sampling, upper and lower sides of leaves; parasitized; killed by predators, lower sides of leaves, total), and summer larvae (3rd sampling), in the 1958-59 generation, which did not differ significantly. The ratios of the density in the upper to that in the lower level ranged from 0.8 to 6.0. Although percentage egg predation for upper and lower crown levels was 1.8 and 2.5 per cent respectively in the 1957-58 generation, 10.3 and 4.73 (1st sampling) and 17.8 and 15.3 per cent (2nd sampling) respectively in the 1958-59 generation, the differences were not statistically significant. Percentage mortality of winter larvae attributable to predation by birds was 10 per cent greater in the upper than in the lower crown level. This is reflected in a reversal of crown level density ratios of the prey from 1.4 to 0.8.

Densities differed between quadrants for spring larvae of the 1956-57 generation, and summer larvae (2nd sampling), winter larvae (1st sampling), spring larvae (2nd sampling, No. on clusters without blossoms), and pupae of the 1957-58 generation. Also, for summer and for winter larvae of the 1957-58 generation (2nd sampling in each stage) the ratios of the density in the upper to that in the lower crown level varied between quadrants from 1.1:1 for the south to 1.4:1 for the west.

The egg counts from the upper sides of the leaves were almost four times as high, on the average, as counts from the undersides, in the 1957-58 generation, and five times as high in the 1958-59 generation.

A combined analysis of all counts of summer larvae of the 1957-58 generation before they moved to the twigs, i.e., the first three samplings (56, 57, 64; Table V), and of winter larvae (59, Table V) showed no change in mean larval density from the time of hatching to hibernation. This was also true for summer larvae of the 1958-59 generation (Table V, first four samplings, 24, 25, 25, 24; winter larvae, 21). The ratios of the density in the upper to that in the lower crown level increased during these samplings for the 1957-58 generation but showed a slight decrease for the 1958-59 generation (Table III).

Larval counts (Table V) just before and during movement to the bud clusters indicated that for the 1957-58 generation on September 23-26, i.e., at the fourth sampling, an average of only 47 per cent of larvae from the upper-crown level had hibernated as compared with 56 per cent for the lower-crown level. Larval counts, fourth sampling, September 11-15, for the 1958-59 generation did not indicate larvae to have hibernated from either crown level. As of June 17, 59 ± 1.5 per cent of spring larvae of the 1956-57 generation had moved with their cases to the ground cover to pupate; as of June 9, 28 ± 2 per cent of the 1957-58 generation had similarly moved.

For both generations, movement of larvae to the ground cover did not take place after these dates.

The distribution of percentage predation of eggs of the 1957-58 generation was tested for uniformity by comparing its variance with the binomial variance. Although no consistent differences between crown levels were found, the intra-tree variance was greater than the binomial variance by a factor of 2.7, indicating that the probability of being attacked was not uniform for all eggs. Inter-tree variance was appreciably greater even than this, but there was no apparent association between percentage predation and prey density.

TABLE IV

Estimates of mean densities and of variations between samples of immature stages of *S. ocellana* in three generations, a sample of 25 leaf or bud clusters being taken from each of eight sections from each of 20 trees

Generation and stage	Mean number per sample, $\bar{x}$	Variance component	
		Within trees, s^2_s	Between trees, s^2_t
1956-57 Generation			
Winter larvae, in hibernacula			
1st sampling, early April, '57 occupied			
Total	1.44±0.11[1]	1.84	0
Killed by frost	1.01±0.10 (70%)	1.46	0
2nd sampling, October[2], '57			
Killed by frost	1.29±0.19 (90%)	2.65	0.37
Spring larval shelters			
1st sampling, late April during movement to leaf clusters, occupied	0.43±0.05	—	—
2nd sampling, early May, occupied	0.68±0.13	1.15	0.21
Pupal shelters, mid June, occupied	0.63±0.05	0.43	0
1957-58 Generation			
Eggs, mid July			
Upper sides of leaves	5.81±0.45	—	—
Lower sides of leaves	2.90±0.21	—	—
Total	8.71±0.64	22.09	5.54
Parasitized	2.73±0.13 (33%)	2.62	0
Summer larval shelters			
1st sampling, late July, occupied	3.76±0.42	6.57	2.73
2nd sampling, early August, occupied	3.76±0.38	6.27	2.05
3rd sampling, mid August not all occupied	5.76±0.54	—	—
4th sampling, late August, not all occupied	7.58±0.56	—	—
5th sampling, late September, not all occupied	9.10±0.51	—	—
Winter larvae, in hibernacula			
1st sampling, October, occupied	3.29±0.25	4.11	0.72
2nd sampling, early April, occupied			
Total	3.77±0.26	4.74	0.72
Killed by frost	0.29±0.04 (8.6%)	0.32	0
Killed by disease	0.06±0.02 (1.8%)	0.05	0
Spring larval shelters			
1st sampling, early May during movement to leaf clusters, occupied			
On clusters with blossoms	1.64±0.11	—	—
On clusters without blossoms	0.04±0.02	—	—
Total	1.68±0.11	—	—
2nd sampling, late May, not all occupied			
On clusters with fruit, occupied	2.31±0.15	—	—
On clusters without fruit, occupied	0.41±0.11	—	—
Occupied	2.72±0.18	2.79	0.31
Not occupied[3]	0.39±0.05 (13%)	0.32	0.02
Total	3.11±0.19	—	—
Pupal shelters, mid June, not all occupied			
In pupal stage	0.08±0.02	—	—
In pre-pupal stage	1.33±0.14	—	—
Occupied	1.38±0.14	1.53	0.23
Not occupied[3]	1.60±0.15 (54%)	1.03	0.35
Total	2.98±0.25	—	—
On clusters with fruit, not all occupied	2.81±0.22	—	—
On clusters without fruit, not all occupied	0.17±0.07	—	—

TABLE IV (*continued*)

Generation and stage	Mean number per sample, $\bar{x}$	Variance component	
		Within trees, s^2_w	Between trees, s^2_t
1958-59 Generation			
Eggs			
1st sampling, mid July			
Upper sides of leaves	14.2±0.82	—	—
Lower sides of leaves	13.7±0.65	—	—
Total	27.9±1.43	133.5	24.4
Parasitized, upper sides of leaves	4.42±0.14	—	—
Parasitized, lower sides of leaves	1.28±0.17	—	—
Total	5.70±0.56 (20%)	15.7	4.42
Killed by predators, upper sides of leaves	0.15±0.04	0.15	0.03
Killed by predators, lower sides of leaves	0.13±0.16	0.12	0.03
Total	0.28±0.09 (1.0%)	0.32	0.15
2nd sampling, early September			
Upper sides of leaves	14.4±1.5	—	—
Lower sides of leaves	19.8±1.5	—	—
Total	34.2±2.2	114.50	5.30
Parasitized, upper sides of leaves	6.63±0.75	—	—
Parasitized, lower sides of leaves	2.75±0.75	—	—
Total	9.38±1.01 (27%)	5.75	1.72
Killed by predators, upper sides of leaves	0.65±0.15	—	—
Killed by predators, lower sides of leaves	0.44±0.10	—	—
Total	1.09±0.20 (3.2%)	1.17	0.02
Summer larval shelters			
1st sampling, late July, not all occupied			
Live larvae	5.60±0.33	10.6	0.86
Killed by predators	1.70±0.14 (2.3%)	2.09	0.14
Occupied	7.30±0.46	12.7	2.80
Not occupied	0.90±0.11	0.82	0.14
Total	8.20±0.52	13.9	3.8
2nd sampling, mid August, not all occupied			
Occupied	8.20±0.15	17.0	2.68
Not occupied	2.50±0.20	26.7	0.49
Total	10.7±0.60	23.3	4.76
3rd sampling, early September, not all occupied			
Occupied	7.20±0.49	9.21	3.80
Not occupied	3.40±0.37	4.80	2.17
Total	10.6±0.75	18.3	9.27
Winter larvae, in hibernacula			
1st sampling, October, occupied			
Total	9.46±0.38	18.0	6.98
Killed by frost[4]	0.86±0.08	1.03	0.26

[1]Standard error.

[3]Larvae killed by frost winter 1956–57 still on the trees.

[2]Mortality largely attributable to predation by birds, see text, section, *Timing of Samples* (spring larvae)

[4]Larvae killed by frost winters of 1956–57, 1957–58, combined, still on the trees.

Both Species.—The analyses of variance indicated that differences between crown levels in particular must be taken into account in sampling of these two species. In a survey in which the object is only to detect gross annual fluctuations in the population density, the sampling of only one level is probably adequate provided that the same level is sampled each year. In life-table studies, however, estimates of absolute population densities at successive stages of the insects' development are required, and therefore the entire height of the tree should be represented in the samples for all stages except possibly the pupae.

TABLE V

Estimates of mean densities and of variations between samples of immature stages of *C. serratella* in three generations, a sample of 25 leaf or bud clusters being taken from each of eight sections from each of 20 trees

Generation and stage	Mean number per sample, $\bar{x}$	Variance component	
		Within trees, s^2_w	Between trees, s^2_t
1956-57 Generation			
Spring larvae			
1st sampling, early May	11.7 ±1.1[1]	63.6	18.0
2nd sampling, early June, migrated to ground cover	7.0 ±1.1	62.0	30.5
Pupae, mid June	4.8 ±0.4	11.6	2.6
1957-58 Generation			
Eggs, mid July			
Upper sides of leaves	57.5 ±3.1	—	—
Lower sides of leaves	15.2 ±1.0	—	—
Total	72.7 ±3.8	576	217
Killed by predators	1.5 ±0.2 (2.3%)	2.9	0.55
Summer larvae			
1st sampling, late July	55.7 ±4.1	202	305
2nd sampling, early August	57.3 ±3.5	173	224
3rd sampling, mid August	63.8 ±3.0	195	159
4th sampling, late September, during movement to bud clusters	30.7 ±1.2	—	—
Winter larvae			
1st sampling, October	59.0 ±3.3	284	188
2nd sampling, early April	8.0 ±0.5	21.8	3.7
Killed[2]	51.0 ±3.3 (86%)	—	—
Spring larvae			
1st sampling, early May	4.9 ±0.3	6.8	0.97
2nd sampling, late May			
On clusters with blossoms	4.1 ±0.2	—	—
On clusters without blossoms	0.9 ±0.1	—	—
Total	5.0 ±0.2	9.5	0
Pupae, mid June			
On clusters with fruit	3.2 ±0.2	—	—
On clusters without fruit	0.4 ±0.08	—	—
Total	3.6 ±0.3	4.2	1.1
Migrated to ground cover	1.4 ±0.1	—	—
1958-59 Generation			
Eggs			
1st sampling, mid July			
Upper sides of leaves	23.4 ±1.2	60.8	21.4
Lower sides of leaves	4.0 ±0.37	10.5	1.54
Total	27.4 ±1.43	89.2	30.2
Parasitized	0.08±0.02 (0.3%)	0.08	0
Killed by predators, upper sides of leaves	2.07±0.48	8.63	3.64
Killed by predators, lower sides of leaves	0.12±0.04	0.28	0
Total	2.19±0.05 (8%)	9.17	3.67
2nd sampling, early September			
Upper sides of leaves	22.8 ±1.3	—	—
Lower sides of leaves	2.4 ±0.45	—	—
Total	25.2 ±1.4	63.4	0
Parasitized	0.09±0.05 (0.3%)	0.05	0
Killed by predators, upper sides of leaves	3.84±0.82	—	—
Killed by predators, lower sides of leaves	0.31±0.20	—	—
Total	4.15±0.80 (16%)	8.30	1.60

TABLE V (*continued*)

Generation and stage	Mean number per sample, $\bar{x}$	Variance component	
		Within trees, s^2_w	Between trees, s^2_t
Summer larvae			
1st sampling, late July	24.0 ±1.5	73.2	36.9
2nd sampling, early August	25.4 ±1.3	177.0	15.7
3rd sampling, late August	25.5 ±1.5	51.5	8.14
4th sampling, mid September	24.6 ±1.8	79.0	61.6
Winter larvae			
1st sampling, October	21.1 ±1.5	71.9	55.7

[1]Standard error.
[2]Mortality largely attributable to predation by birds, see text, section, *Timing of Samples* (winter larvae)

The number of clusters examined at each level should be roughly proportional to the amount of foliage in that level.

Although appreciable differences between quadrants were found in only a few samplings for *S. ocellana* (Table II, 1957-58 generation, eggs, parasitized; summer larval shelters, 5th sampling; spring larval shelters, 2nd sampling, not occupied; pupal shelters, in pre-pupal stage: 1958-59 generation, eggs, 2nd sampling, parasitized, upper sides of leaves; total; summer larval shelter, 3rd sampling, not occupied; total), and for *C. serratella* (Table III, 1956-57 generation, spring larvae; 1957-58 generation, summer larvae, 2nd sampling; winter larvae, 1st sampling; spring larvae, 2nd sampling, on clusters without blossom; pupae, total on clusters), it is strongly recommended that all quadrants be sampled if the results are to be used in life-table studies. Again the number of samples should be approximately proportional to the amount of foliage.

The analyses of egg counts indicated that both sides of the leaves must be examined in life-table studies.

Components of Variance

After the F tests have sorted out those factors that made a demonstrable contribution to the overall variation from those that did not, it is sometimes useful to estimate the magnitudes of some of the contributions. In this study, estimates of the intra-tree (s_w^2) and inter-tree (s_t^2) error variances were calculated and used to determine the optimum number of samples per tree and also the number of trees required to obtain an estimate of population density with a specified standard error.

The inter-tree error variance was obtained from the mean square for trees and the residual mean square by the formula (MST - MSR) ÷ 8; it was assumed to be zero whenever MST was not significant. For example, from the mean squares in Table I, $s_t^2 = (66.4 - 22.1) \div 8 = 5.54$, and $s_w^2 = 22.1$. These components of variance are listed in Tables IV and V for those stages that would ordinarily be sampled in life-table studies of *S. ocellana* and *C. serratella*.

This summarizes the results of the analyses of variance, which can now be applied (a) to determine the reproducibility of the present density estimates, and (b) to make recommendations for sampling procedures in life table studies.

Mean Density and Percentage Error

Estimates of the mean densities and of the effects of a few mortality factors are listed in Tables IV and V along with their standard errors. Each mean repre-

sents observations on eight samples of 25 leaf clusters (or bud clusters) from each of 20 trees. Standard errors were computed from the mean squares for trees by the formula $s_x = \sqrt{MST/160}$, except for those cases in which trees did not differ significantly; here the residual mean squares were used instead. As the data indicate, the standard error was generally of the order of 10 per cent of the mean or less. For *S. ocellana*, exceptions are to be noted in the mean density of spring larvae (1st sampling) of the 1956-57 generation, of winter larvae (2nd sampling, on clusters with fruit, occupied) and pupal shelters (in pupal stage) of the 1957-58 generation, and of eggs (1st sampling, killed by predators, upper sides of leaves; 2nd sampling, killed by predators, upper and lower sides of leaves; total) of the 1958-59 generation, which had a standard error ranging from 18 to 26 per cent; for winter larvae (2nd sampling, killed by disease), spring larval shelters (1st sampling, on clusters with blossoms), pupal shelters (on clusters without fruit, not all occupied) of the 1957-58 generation, and eggs (1st sampling, killed by predators, lower sides of leaves; total) of the 1958-59 generation the standard error ranged from 33 to 50 per cent. Similarly, for the mean density of *C. serratella* pupae (on clusters without fruit) of the 1957-58 generation, and eggs (1st sampling, parasitized; killed by predators, upper sides of leaves: 2nd sampling, lower sides of leaves; killed by predators, upper sides of leaves; total) of the 1958-59 generation the standard error ranged from 19 to 35 per cent, and for eggs (1st sampling, killed by predators, lower sides of leaves: 2nd sampling, parasitized; killed by predators, lower sides of leaves) of the 1958-59 generation from 33 to 64 per cent.

Optimum Number of Samples Per Tree

The procedure for determining optimum allocation of resources in two-stage sampling may be found in a number of statistical books (e.g., Cochran, 1953, Sec. 10.6; Snedecor, 1956, Sec. 17.12). In the present study, trees constituted the primary sampling units and the 25-cluster samples were the secondary sampling units. Using the appropriate values in the formula given by Cochran and by Snedecor gives the estimated number of samples per tree that will minimize the total cost of collection and examination as $n = \sqrt{(S^2_s/S^2_t)(C_t/C_s)}$ where S^2_s and S^2_t are the intra- and inter-tree variance components, C_t is the cost of moving from one tree to another, and C_s is the cost of taking and examining one sample of 25 clusters.

A summary of the calculations leading to η is given in Table VI. The ratios of the variance components for each stage (Tables IV and V) were averaged for the two species, and sometimes for a number of samplings of the same stage of either species. For example, in the egg sampling data, the ratio was 4.0 for the total egg counts of *S. ocellana*, 2.7 for the total egg counts of *C. serratella*, and 5.3 for the number of eggs of the latter killed by predators; their average value, 4.0, was used in determining η for the egg stage. For counts of parasitized eggs of *S. ocellana* (Table IV), the estimate of S_t^2 was zero. On the basis of this estimate, there would be no advantage, for these counts, in allocating the samples to more than one tree. However, instead of assigning an arbitrarily large ratio of variance components to these counts, η was calculated from the other three ratios only (and later rounded to the next higher integer; Table VII).

With 20 trees the total time required to walk from tree to tree and to prepare for sampling at each tree was about one day for each stage, or 24 minutes per tree. The time required for two men to take and examine 160 samples was

TABLE VI

Estimation of numbers of 25-cluster samples per tree required to minimize cost of collection and examination for immature stages of *S. ocellana* and *C. serratella*[1]

Stage	Mean ratio[2] of Variance components, s^2_s/s^2_t	Cost ratio[3] C_t/C_s	No. of samples $n = \sqrt{\left(\frac{s^2_s}{s^2_t}\right)\left(\frac{C_t}{C_s}\right)}$
Eggs	4.0	0.5	1.4
Summer larvae	1.9	2.0	1.9
Winter larvae	5.5	0.7	2.0
Spring larvae	8.6	4.0	5.9
Pupae	3.4	2.0	2.6

[1]For simultaneous sampling of *S. ocellana* and *C. serratella*; for a single species, multiply n by $\sqrt{2}$.
[2]Omitting ratios in which $s^2_t = 0$.
[3]C_t, cost of moving from one tree to another and preparing for sampling; C_s, cost of taking and examining one sample.

estimated to be 17 days for eggs and 11 days for winter larvae. For the other samplings the clusters were not removed from the tree; examination alone required four days for summer larvae, two days for spring larvae, and four days for pupae. In the egg stage, therefore, it took an average of 51 minutes to take and examine a sample, i.e., $C_s = 51$. Since $C_t = 24$, the cost ratio was 0.5 for the egg stage. These cost figures are applicable to a joint sampling of the two species. If only one species is to be sampled, C_s will be approximately halved while C_t will remain the same; the tabulated η is then multiplied by $\sqrt{2}$.

On the basis of these calculated η values, it is recommended that two 25-cluster samples per tree be examined in the egg and in the summer larval stages, but that three samples be examined in the winter larval and the pupal stages and six in the spring larval stage. Since the standard error is obtained directly from the mean square for trees, it would ordinarily be unnecessary to take the two (or three or six) samples separately; instead, a single sample of 50 (or 75 or 150) clusters might be taken. As indicated in a previous section, the sample should be taken in such a way that it represents all crown levels and quadrants.

Number of Trees to Sample for a Specified Precision

In planning projects involving sampling, attention must be given to the amount of sampling that is likely to be required for a specified precision in the estimate of the mean. Precision requirements may, of course, vary from one project to another. In life-table studies on the spruce budworm, *Choristoneura fumiferana* (Clem), Morris (1955) specified a 10 per cent standard error in his estimates of mean density, and this specification seems satisfactory for the orchard insects studied here. Estimates of the number of trees required for a 10 per cent standard error were accordingly calculated (Table VII).

The coefficients of inter-tree variation, based on integral values of η, the number of 25-cluster samples per tree from the preceding section, were calculated from the components of variance and the means (Tables IV and V), as follows:

$$C.V._n = \frac{100}{\bar{X}} \sqrt{\frac{S^2_s}{n} + s^2_t}$$

For example, for numbers of eggs of *S. ocellana*:

$$C.V._{\bar{x}} = \frac{100}{8.71}\sqrt{\frac{22.09}{2} + 5.54} = 47\%$$

The number of trees, n_t, required for a standard error of p per cent may be derived from the coefficient of inter-tree variation as $n_t = (C.V._{\bar{x}}/p)^2$. For a 10 per cent error in mean number of eggs of *S. ocellana*, for example, a total of $(47/10)^2$, or 22, trees should be sampled, with 50 clusters per tree.

TABLE VII

Estimation of numbers of trees to be sampled for a 10 per cent error, on the basis of n 25-cluster samples, for immature stages of *S. ocellana* and *C. serratella*

Stage	No. of samples per tree	*S. ocellana*		*C. serratella*	
		C.V.[1]$_{\bar{x}}$	n_t[2]	C.V.$_{\bar{x}}$	n_t
Eggs	2				
Total					
1957-58		47	22	31	10
Killed by parasitism or predation		42	18	93	86
1958-59		34	11	31	10
Killed by predators		198	395	131	171
Parasitized		61	37	250	625
Summer larvae	2				
Total					
1957–58, 1st sampling		65	42	36	13
" ", 2nd sampling		61	37	31	10
" ", 3rd sampling				25	6
1958–59, 1st sampling		39	15	35	12
" ", 2nd sampling		37	14	40	16
" ", 3rd sampling		40	16		
" ", 4th sampling				41	16
Winter larvae	3				
Total					
1957–56		54	30		
1957–58, 1st sampling		44	19	28	8
" ", 2nd sampling		40	16	41	17
1958–59, 1st sampling		38	14	42	17
Killed by frost					
1956–57, 1st sampling		69	48		
" ", 2nd sampling		87	75		
1957–58		113	127		
Killed by disease, 1957–58		68	46		
Spring larvae	6				
Total					
1956–57		94	88	46	21
1957–58, 1st sampling				30	9
" ", 2nd sampling		32	11	25	6
Unoccupied shelters		68	47		
Pupae	3				
Total					
1956–57		61	37	52	27
1957–58		62	39	45	20
Unoccupied shelters		52	27		

[1]Coefficient of variation (inter-tree), on the basis of n 25-cluster samples per tree, $\frac{100}{\bar{x}}\sqrt{\frac{s^2_a}{n} + s^2_t}$.

[2]Number of trees required, $\left(\frac{C.V._{\bar{x}}}{10}\right)^2$.

These calculated values of n_t are applicable to orchards that are roughly similar in size and uniformity to the orchard sampled in this study. It is advisable to partition the orchard into blocks if marked gradients of infestation may be expected. In the partitioning, an attempt should, of course, be made to minimize the variation within blocks. If block size varies appreciably, the number of trees to be sampled in each should be roughly proportional to the size of the block, if the variation is similar in the various blocks.

The above formula for n is appropriate when only a small fraction of all trees in the orchard are to be sampled. This was the case in the present study. However, if more than one-tenth of all the trees are needed to attain the desired precision, a 'finite population correction' (Cochran, 1953, Sec. 2.5 and 4.5; Hansen *et al.*, 1953, Sec. 4.11; Snedecor, 1956, 17.6) should be applied.

Suggested Sampling Plan

Though the values of n_t were estimated (Table VII) for single variables, what is usually needed in practice is a combined estimate for all variables studied at any one stage, e.g., 'total number of eggs' and 'number of eggs killed by predators'. This may or may not be similar for the two species. When more than one variable is to be examined, the usual procedure according to Hansen *et al.* (1953, Sec. 4.11) is to take a sample large enough for the most important variables, and then accept whatever precision is attained for the less important ones. Applying this principle to the n_t values in Table VII and rounding upwards to the nearest multiple of 5 leads to the numbers of trees shown in Table VIII. Along with these are listed the numbers of clusters per tree on which they are based. For example, in sampling for eggs of *S. ocellana*, it is suggested that 25 trees be taken at random and that a 50-cluster representative sample from each tree be examined.

The n_t values in Table VII indicate that the error in mean number of eggs of *C. serratella* killed by predators may be considerably greater than 10 per cent when only 10 trees are sampled. The percentage standard error, p, is $C.V.n./\sqrt{n_t}$, which is $93/\sqrt{10}$ or 29, for these egg mortality data if ten trees are sampled. As a compromise the number of trees might be increased to 25; this would reduce the estimated standard error to 18 per cent for numbers of eggs killed and 6 per cent for total number of eggs. For numbers of winter larvae of *S. ocellana* killed by frost, the error is 14 to 17 per cent for the 1956-57 generation and 23 per cent for the 1957-58 generation if 25 trees are sampled. Therefore, with the possible exception of the egg stage of *C. serratella* and the winter larval stage of

TABLE VIII

Suggested sampling plan for life-table studies of *S. ocellana* and *C. serratella*

Stage	No. of clusters per tree	No. of trees	
		S. ocellana	*C. serratella*
Eggs	50	25	10
Summer larvae	50	40	15
Winter larvae	75	25	15
Spring larvae	150	50	15
Pupae	75	40	25

S. ocellana, the sample plans outlined in Table VIII would be expected to provide a reasonable degree of precision for life-table studies on these two species, unless densities differ markedly from those reported here.

Morris (1955, Sec. 12.5) found that the amount of sampling required for a specified percentage error increased as population density decreased. For sampling distributions of the negative binomial type, this is always so since the coefficient of variation is a function of the reciprocal of mean density. Since this type of distribution is common in insect sampling, it is likely that the number of trees to be sampled for very low population densities would be higher than recommended here (Table VIII), and conversely for high densities.

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Collection, Extraction, Sterilization and Low-Temperature Storage of Black-Fly Eggs (Diptera : Simuliidae)[1]

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Because black flies are active for only a few months each year in the vicinity of this laboratory, methods for collecting, extracting, sterilizing, and storing eggs were devised to facilitate a year around program of research. These methods were developed partly from existing entomological and limnological techniques.

Collecting Eggs

The eggs of *Cnephia dacotensis* D. & S., *Simulium aureum* Fries, *S. vittatum* Zett., *S. decorum* Walk., and *S. venustum* Say, species which lay their eggs in masses on objects at the water surface, were usually found and collected easily during the egg-laying season of June, July and August.

S. arcticum Mall. oviposits in flight and the eggs were readily collected either from the river surface or from the river bottom where they eventually lodged in the sand and mud. (Fredeen et al, 1951). The eggs of *S. meridionale* Riley and *S. luggeri* N. and M. were also recovered from river-bed samples, indicating that these species may oviposit in flight. It is interesting to note that the eggs of *C. dacotensis, S. aureum, S. decorum* and *S. venustum* were also frequently recovered from river- or stream-bed samples. Some of these eggs may have originated from disintegrated egg masses, although Davies and Peterson (1956) observed *S. decorum* ovipositing while in flight.

A plankton net was used for surface collecting but a shovel or dredge was required for bottom sampling.

The Ekman dredge, a light-weight dredge, was used successfully only in slowly flowing streams with soft bottoms. In fast-flowing streams the heavier Petersen dredge was required but even this instrument had to be weighted to ensure that it would settle readily to the bottom and remain upright. For sampling through the ice in the winter a Petersen dredge was used where the water was more than three feet deep; in shallower water a hoe with side walls welded on the blade was often used.

During transportation to the laboratory the eggs were usually kept in ice water to avoid hatching, or loss of viability from overheating.

Extracting Eggs From Dredged Detritus

Brine flotation was used to extract eggs from sand or other material dredged from a stream bed. This is an adaptation of a method for extracting wireworms from soil samples by flotation in a solution of magnesium sulphate (Ladell, 1936).

Various concentrations of sodium chloride were tested and although the eggs floated to the surface of a solution that was only 30 per cent saturated, 80 to 100 per cent saturated solutions were used when it was discovered that a brief exposure to such concentrations was not harmful to the eggs. This solution was prepared by adding about one unit of sodium chloride to four units of water. However, the exact amounts depended upon the water content of the dredged material. If a hydrometer was not available, the appearance of chironomid or other aquatic larvae on the surface indicated that sufficient salt had been added.

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Efficient extraction of the eggs required that the dredged material be thoroughly dispersed in the brine. This could be done satisfactorily simply by stirring the material in the brine in a large tub with a hoe. However a simple churn, consisting of a five-gallon can with a tight lid, rotated on a pair of rollers, was usually used at the Saskatoon laboratory. The can was filled about two-thirds full with a fluid mixture of dredged material, water and about 10 pounds of salt and then rotated at about 20 r.p.m. 100 times in a horizontal position and 30 times in a 45° position. The mixture was then allowed to stand for a few minutes before the floating organic material was poured through a series of three or more screens. Screens of stainless steel wire were found to be more durable and less readily plugged than nylon screens. The coarsest screen was placed at the top to retain particles larger than black-fly eggs which ranged in diameter from 0.2 to 0.3 mm. and in length from 0.3 to 0.4 mm.; the bottom screen had openings of about 0.1 mm. in diameter to retain the eggs; the need for intermediate screens depended upon the amount of organic detritus floating on the brine. Fresh water was poured through the screens until all traces of salt were removed; the eggs were damaged by plasmolysis if kept in the 80 per cent brine solution for more than about one hour.

A second brine extraction was often required to remove additional detritus from the eggs after which the eggs were sorted under a microscope with the aid of a small syringe drawn to a fine tip.

The eggs of seven species of black flies, identified by rearing to adults in the laboratory, were obtained by dredging and brine flotation. These included *C. dacotensis*, *S. aureum*, *S. meridionale*, *S. articum*, *S. decorum*, *S. luggeri* and *S. venustum*. Only a few eggs of some species were obtained in this manner but as many as 14,000 eggs of *C. dacotensis*, 580 eggs of *S. venustum* and 76 eggs of *S. arcticum* were recovered from single cubic foot samples.

Sterilizing Eggs

Tests indicated that the most effective and least harmful method of sterilizing the eggs was to soak the egg masses in five per cent sodium hydroxide. This is one of three chemicals commonly used to disinfect fly eggs when rearing maggots for surgical use (Galtsoff et al 1937).

Black-fly egg masses started to disintegrate, simultaneously with disappearance of the matrix, after they were soaked for about 40 minutes to one hour in the sodium hydroxide solution. However a three-hour treatment was required to produce 100 per cent sterility as determined by the culture of series of samples on nutrient agar. The sodium hydroxide treatment also increased percentage hatch in many tests and apparently speeded up embryonic development, possibly as a result of disintegration of the egg masses. Keeping qualities during low temperature storage were also improved.

Percentage hatch and duration of the egg stage of untreated and treated eggs of *S. venustum* and *S. vittatum* Zett. were as follows:

	Number of samples	Hatch (%)		Duration of egg stage (days)	
		Range	Average	Range	Average
Untreated	8	27–81	51	15–40+	29+
Treated	31	45–92	72	4–26	13

Each sample consisted of about 10,000 eggs. Unfortunately the eggs of these two species occurred together in these samples and thus it was not determined if they reacted differently to treatment.

Mercuric chloride proved unsatisfactory for sterilizing eggs. A 0.1 per cent solution killed the eggs in 15 seconds, whereas a two-minute treatment was required to sterilize the eggs. Furthermore the mercuric chloride did not dissolve the matrix surrounding the eggs.

Low Temperature Storage

At room temperatures (25 to 30° C.) the eggs of *S. venustum* and *S. vittatum* commenced to hatch in about four days and even at temperatures as low as 3.0° C. the eggs of these and several other species continued embryonic development. Tests showed, however, that at 0.5 to 1.5° C. these eggs could be kept unhatched but viable for an extended period of time. Prior to storage the eggs were generally sterilized as described and then small quantities were placed in sterile water or on sterile damp filter paper in sealed jars. Some data on the viability of eggs of *S. venustum* and *S. vittatum* thus stored for various periods of time are shown in Table I.

TABLE I

Viability[1] of eggs of *S. venustum* and *S. vittatum* after various intervals of storage at 0.5 to 1.5° C.

Species	Date eggs collected	Sterilized with 5 % NaOH	Storage period (weeks)											
			0	0.5	1.0	3	8	12	16	17	21	39	56	140
			Viability (per cent)											
S. venustum	June 17, 1955	Yes	81	—	—	—	—	—	—	62	61	48	35	—
	Aug. 6, 1956	Yes	—	—	—	—	—	—	—	—	—	—	—	0.01
S. vittatum	July 21, 1955	No	46	51	59	34	30	0.1	0	—	—	—	—	—
	July 21, 1955	Yes	34	—	41	20	7	3	>0.1	—	—	—	—	—

[1]As determined by the percentage that hatched.

A large percentage of the eggs of *S. venustum* remained viable for a year and a small percentage for as long as 2.5 years. *S. vittatum* eggs remained viable for a much shorter period of time. These results were to be expected, since in the vicinity of this laboratory *S. venustum* overwinters in the egg stage at 0° C., whereas *S. vittatum* overwinters in the larval stage. The observed increase in the percentage hatch of *S. vittatum* eggs following 0.5 to one week of exposure to near-freezing temperatures may be an adaptation that ensures the overwintering of an adequate population of larvae.

Larvae from these four batches of eggs and from others similarly treated were used in numerous laboratory investigations. Survival and vitality of the larvae and adults produced from them did not noticeably differ from those from freshly-collected eggs.

In other tests the eggs of *C. dacotensis*, *S. arcticum*, *S. aureum*, *S. decorum*, *S. luggeri* and *S. meridionale* also remained viable when stored at 0.5 to 1.5° C. for periods of two to nine months. Some of these species at least are known to overwinter in the egg stage in this region. Undoubtedly other species native to the Temperate and Arctic zones also overwinter as eggs and could thus be similarly stored in the laboratory.

An unsuccessful attempt was made to store the eggs of *S. venustum* and *S. vittatum* at —79° C., using the technique developed for the preservation of viable bull semen by Polge and Lovelock (1952).

A small proportion of eggs of *C. dacotensis* remained viable when stored at 19.5 to 22° C. for 8.5 months. However this species normally spends much of the summer in the egg stage.

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Description and Life History of a New Species of *Cinara* (Homoptera: Aphididae) from *Pinus banksiana* Lamb.[1]

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Aphids of the species herein described as new can be readily distinguished from all other species in the genus *Cinara* by the unusual length of the unguis. The feeding site is also characteristic; this is the only species in the genus known to feed on the roots of *Pinus banksiana.*

The species was first collected in 1956 at Lac La Ronge, Saskatchewan, by B. B. McLeod, of the Winnipeg Laboratory. In 1957 it was found by the authors at Cedar Lake, thirty miles north of Vermilion Bay, Ontario, where observations on the life history of the species were carried out.

The junior author contributed the method of rearing the aphids in the insectary, and some of the data on the life history.

***Cinara piniradicis* Bradley, n. sp.**

Fundatrix

Colour pinkish-brown to dark brown dorsally, bluish-grey ventrally. *Measurements* (in mm.).—Three specimens were measured. Length of body, 4.42-4.57. Width of head across eyes, .74-.82. Antenna, total length, 1.79-1.98; length of segments, III, .78-.85; IV, .27-.29; V, .35-.39; VI, base, .14-.16; unguis, .07-.08. Number of sensoria on antennal segments, III, 1; IV, 1; V, 2. Rostrum, total length, 2.54-2.75; length of segments, IV, .29-.30; V, .114-.115. Hind tibia length, 2.83-3.24; width, .10-.11. Length of hind tarsal segments, I, .116-.136; II, .32-.34. Diameter of cornicle base, .46-.57. Length of setae, on antenna, .038-.043; on dorsum of abdomen, .049-.051; on hind tibia .034-.043.

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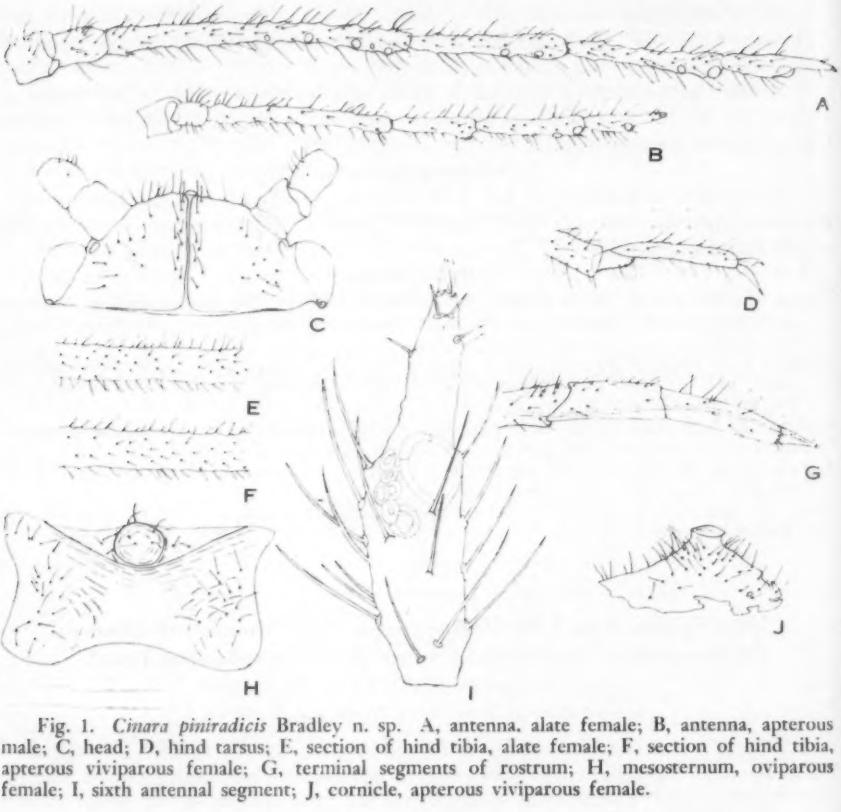

Fig. 1. *Cinara piniradicis* Bradley n. sp. A, antenna, alate female; B, antenna, apterous male; C, head; D, hind tarsus; E, section of hind tibia, alate female; F, section of hind tibia, apterous viviparous female; G, terminal segments of rostrum; H, mesosternum, oviparous female; I, sixth antennal segment; J, cornicle, apterous viviparous female.

Alate viviparous female

Colour dark brown, without waxy secretions. In cleared specimens the antenna is fuscous, with the exception of a small light brown portion at the base of III. Legs dark brown. The central portions of the mesothoracic tibiae are faintly lighter than the rest. Cornicles and cauda dark brown. Dorsum of abdomen transparent except for the longitudinal rows of muscle attachment plates; two small rectangular sclerotized areas, one on either side of the median line, on the first abdominal segment; and two narrow transverse sclerotized areas on the seventh and eighth segments. All these areas are dark brown.

Measurements.—Average, number of specimens, and range: Length of body, 3.79 (6) 3.43-4.19. Width of head across eyes, .73 (6) .68-.80. Antenna, total length 2.09 (5) 1.94-2.19, length of segments, III, .78 (5) .70-.84; IV, .36 (5) .33-.38; V, .44 (5) .42-.49; VI, base, .16 (5) .14-.18; unguis, .095 (5) .08-.10. Number of sensoria on antennal segments, III, 4 (5) 3-5; IV, 1 (5) 1-2; V, 2. Rostrum, total length, 3.41 (4) 3.34-3.49; length of segments; IV, .316 (6) .30-.32; V, .115 (5) .111-.122. Length of forewing, 4.21 (6) 3.60-4.46. Hind tibia, length, 3.36 (6) 3.01-3.54; width, .089 (6) .076-.099. Length of hind tarsal segments, I, .123 (6) .110-.135; II, .36 (6) .34-.37. Diameter of cornicle base, .47 (6) .38-.52. Length of setae, on antenna, .041 (5) .040-.043; on dorsum of abdomen, .042 (6) .038-.045; on hind tibia, .42 (6) .039-.044.

Apterous viviparous female

Colour similar to that of the alate female. The rectangular sclerotized areas on the dorsum of the first abdominal segment are larger than in the alate female, and the transverse band present on the seventh abdominal segment of the alate is made up of numerous small, discrete areas of sclerotization in the apterous female. The remainder of the abdomen is clear, except as noted in the alate female. A large mesosternal tubercle, bearing a few long setae, is present (Fig. 1H).

Measurements.—Apterous females of the second, third, fourth, and fifth generations were measured. No significant differences in measurements were discovered between representatives of these summer generations. Length of body 4.31 (14) 4.03-4.78. Width of head across eyes, .78 (18) .76-.83. Antenna, total length, 2.16 (18) 2.06-2.28; length of segments, III, .87 (19) .82-.94; IV, .36 (19) .32-.41; V, .44 (19) .40-.48; VI, base, .15 (19) .14-.16; unguis, .08 (19) .07-.09. Number of sensoria on antennal segments, III, 2 (19) 1-2; IV, 1 (19) 1-2; V, 2 (19) 2-2. Rostrum, total length, 2.98 (8) 2.75-3.21; length of segments, IV, .32 (19) .29-.34; V, .11 (19) .10-.12. Hind tibia, length, 3.61 (19) 3.37-3.81; width, .12 (19) .11-.12. Length of hind tarsal segments, I, .123 (19) .121-.125; II, .35 (19) .34-.37. Diameter of cornicle base, .54 (20) .42-.59. Length of setae, on antenna, .043 (19) .038-.048; on dorsum of abdomen, .051 (20) .046-.056; on hind tibia, .040 (20) .035-.049.

Oviparous Female

Colour of body and appendages similar to that of the apterous viviparous female. The hind tibia is not swollen, and lacks the sensoria-like structures found on this segment in the oviparous females of many other species. The pericaudal wax ring is also lacking. A large mesosternal tubercle is present, as in the apterous viviparous female. The measurements of the body and appendages in the oviparous female are about the same as those of the apterous viviparous female.

Male

The male is apterous, elongate in form, and small. The colour of the body is yellowish-brown.

Measurements.—Three specimens were measured. Length of body, 2.79. Width of head across eyes, .52-.69. Antenna, total length, 1.47-1.55; length of segments, III, .45-.53; IV, .21-.29; V, .31-.33; VI, base, .14-.15; unguis, .09. Number of sensoria on antennal segments, III, 1-3; IV, 1-3; V, 2-4. Rostrum, total length, 2.59; length of segments, IV, .26; V, .090-.097. Hind tibia, length, 1.80-1.97; width, .072-.075. Length of hind tarsal segments, I, .091-.105; II, .23-.28. Diameter of cornicle base, .12-.14. Length of setae, on antenna, .032-.036; on dorsum of abdomen, .029-.034; on hind tibia, .072-.075.

Egg

The egg is slightly kidney-shaped, shiny black in colour, and does not have waxy filaments or powder on its surface.

Rearing Methods

The roots of small jack pines about four feet in height, and growing in sandy soil, were prepared as follows: each root was cut so that about five inches of the lower stem remained above the root collar. The roots were then cut off close to the collar, washed to remove particles of soil and loose bark, and the stem with its supporting root stubs placed in the bottom of a four-inch petri dish. The stubs of the roots in the dish were covered with a layer of moist cotton batting, over which was placed a disk of paper towelling with a hole

cut in the centre for the stem. A 48-ounce juice can, open at the lower end, and with small holes punched in the upper end, was inverted over the roots, covering the petri dish. Fresh roots were needed every 16 to 18 days.

Aphids for rearing were obtained by pulling four-foot jack pines by hand and examining the roots. The specimens selected were prodded gently until they became disturbed, at which time they withdrew their stylets from the bark and began to move about. They were then transferred to the roots in the petri dishes by means of forceps.

It was found that the roots could be uncovered for about two minutes without the light disturbing the aphids. It was therefore possible to make frequent observations. Cast skins were easily found on the paper towel disks, and this greatly aided observations of the time of moulting and the number and duration of the various instars. The aphids fed mainly on the stem just above the root collar. No loss in size or vigour was observed in the reared aphids as compared to those in the wild population.

Life History

The eggs were laid on the needles of the current season's growth at the ends of the lower branches. They occurred singly, each attached by its slightly concave ventral surface to the inner face of a needle at the point where the two needles began to diverge above the fascicle sheath. This oviposition site was indicated by the position of the egg remains on branches near fundatrices found in the field, and was later corroborated by observing some of the reared oviparous females that were placed on a tree and allowed to oviposit. Hatching was not observed, but fundatrices in the second and third instars were found in small groups under bark scales on the lower trunks of two host trees, one three and the other five inches in d.b.h. The fundatrices changed their positions several times during their development, progressing down the trunks to the roots. They were attended by numerous ants. Full-grown fundatrices with their nymphs were found in colonies on the roots of small trees. Some of the nymphs were reared on cut roots in the insectary, where they passed through five generations, indicating a total of six generations including the fundatrices, of this species during the season. Two alate viviparous females were produced in the third generation. The oviparous females and males appeared in the sixth generation. The fundatrices were first observed on May 15, and some were still producing nymphs on June 28. The periods during which the succeeding generations were reared are as follows: second, June 11-June 29; third, June 29-July 25; fourth, July 25-August 12; fifth, August 12-September 18. Three first-instar nymphs from the fourth, fifth, and sixth generations were reared individually. They moulted four times, passing through five instars in every case. The nymphs spent four days in each of the first three instars and five days in the fourth.

Host

Pinus banksiana Lamb.

Type

Holotype, alate viviparous female collected at The Pas, Manitoba, July 9, 1957, deposited in the Canadian National Collection, Ottawa. Paratypes in the C.N.C. and in the custody of the authors.

Distribution

Collected at Lac La Ronge, Saskatchewan, The Pas, Manitoba, and Perrault Falls in northwestern Ontario.

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